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ANATOMY AND EVOLUTION OF CHIROCENTRID FISHES

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ABBREVIATIONS FOR FIGURES

A.s.——accessory scale.
a.f.——auditory fenestra.
ant.cer.v.——foramen for anterior cervical vein.
Autang.——autangular.
Boc.——basioccipital.
bpt.pr.——basipterygoid process.
Br.——branchiostegal rays.
Bsp.——basisphenoid.
Cl.——cleithrum.
Cm.——coronomeckelian.
Cor.——coracoid.
Dermang.——dermangular.
Dent.—dentary.
Dsph.——dermosphenotic.
d.oss.br.——depression for osseous brushes.
Ect.——ectopterygoid.
eff.ps.a.——foramen for efferent pseudobranchial artery.
Epo.——epiotic.
Eth.——ethmoid.
Exo.——exoccipital.
f.hym.VII——foramen for hyomandibular branch of 7th nerve.
f.m.——foramen magnum.
Fr.——frontal.
Hym.——hyomandibular.
hym.f.——hyomandibular fossa.
inf.f.——infundibular fossa.
Int.——intercalar.
int.car.a.——foramen for internal carotid artery.
Io.——infraorbital.
Iop.——interoperculum.
io.c.——infraorbital sensory canal.
La.——lacrymal.
lat.head v.——lateral head vein.
lat.temp.f.——lateral temporal fossa.
Max.——maxillary.
md.c.——mandibular sensory canal.
Mes.——mesopterygoid.
Mpt.——metapterygoid.
myo.——myodome.
Na.——nasal.
occ.br.——occipital branch of sensory canal.
occ.n.——occipital nerve.
on.a.——foramen for orbitonasal artery.
Op.——operculum.
Ors.——orbitosphenoid.
ot.VII.——foramen for otic branch of 7th nerve.
Pal.——palatine.
Par.——parietal.
Pareth.——parethmoid.
Pas.——parasphenoid.
pe.f.——preepiotic fossa.
Pmx.——premaxillary.
Po.——postorbital.
Pop.——preoperculum.
pop.c.——preopercular sensory canal.
p.pal.VII.——foramen for posterior palatine branch of the 7th nerve.
Pro.——prootic.
pro.br.——prootic bridge.
pt.VII.——foramen for pretrematic branch of 7th nerve.
Ptcl.——postcleithrum.
Ptm.——post-temporal.
ptm.gr.——post-temporal groove.
ptm.f.——post-temporal fossa.
Pto.——pterotic.
Pts.——pterosphenoid.
Qu.——quadrate.
Ra.——retroarticular.
Sb.——scale bone.
sb.br.VII.——foramen for sensory canal branch of 7th nerve.
Sc.——scapula.
Scl.——supracleithrum.
Sclr.——sclerotic.
se.f.——subepiotic fossa.
Smx.——supramaxillary.
So.——supraorbital.
Soc.——supraoccipital.
so.c.——supraorbital sensory canal.
Sop.——suboperculum.
Sph.——sphenotic.
st.IX.——foramen for supratemporal branch of 9th nerve.
stm.f.——subtemporal fossa.
sup.op.V,VII.——foramina for superficial ophthalmic branches of 5th and 7th nerves.
Sym.——symplectic.
tem.c.——temporal sensory canal.
t.f.——temporal foramen.
trig.fac.ch.——trigeminofacial chamber.
Vo.——vomer.
I——foramen for olfactory nerve.
II——foramen for optic nerve.
III——foramen for oculomotor nerve.
IV——foramen for trochlear nerve.
V——foramen for trigeminal nerve.
VI——foramen for abducens nerve.
VII——foramen for facial nerve.
IX——foramen for glossopharyngeal nerve.
X——foramen for vagus nerve.

ABSTRACT

The geologic range of the Chirocentridae exceeds that of other teleostean families. Chirocentrids appear in the Oxfordian (Late Jurassic) and perhaps as early as the Bathonian (Middle Jurassic). In the Cretaceous this family became generically diversified. One genus exists today. Specimens of chirocentrids are known from North, Central and South America, England, Europe, Africa and Australia as well as the Indo-Pacific Ocean.

Descriptive and taxonomic studies of most chirocentrids are scattered in pre-1900 literature. For the first time the entire family is reviewed. Anatomy of the Recent species *Chirocentrus dorab* and the Cretaceous species *Xiphactinus audax, Ichthyodectes ctenodon* and *Gillicus arcuatus* is described with emphasis on neurocranial and jaw structure. Systematics of the 11 other genera included in the Chirocentridae are reviewed.

Two major radiations occurred in the evolution of chirocentrid fishes. The first took place in the Jurassic with the origin of *Allothrissops, Thrissops, Mesoclupea,* and *Pachythrissops.* The second radiation occurred in the Cretaceous with the development of two branches from *Thrissops.* The first branch includes *Eubiodectes, Proportheus* and *Chirocentrus.* The second branch comprises *Spathodactylus, Prymnetes, Cladocyclus, Gillicus, Ichthyodectes, Chirocentrites,* and *Xiphactinus.*

Chirocentrids generally have been thought to be derived from leptolepids. But neurocranial and jaw structure of Mesozoic chirocentrids is more like that of pholidophorids than leptolepids. Therefore chirocentrids, along with elopids, are placed among philodophorid descendants. Leptolepids are ancestral to clupeids, clupavids, and dussumierids.

INTRODUCTION

Fishes of the superorder Teleostei appeared in the Middle Jurassic but it was not until the Late Cretaceous that teleosts became numerous and taxonomically diversified. From their first appearance until the present, teleostean evolutionary history covers a period of approximately 140 million years. The fossil record of teleostean fishes is incomplete and no continuous phylogenetic sequence of any family is preserved. Many existing families are not represented in the fossil record. A few families are known only from their fossil record. Fossil teleosts pertaining to a single family are frequently limited in number of individuals. Commonly these individuals are preserved in such a manner that structures deemed taxonomically important cannot be examined. Consequently, phylogenetic studies of teleostean higher categories generally have been confined to living fishes. In this paper an effort is made to unite morphologic evidence from living and fossil genera in the study of anatomy and evolution of one teleostean family.

The Chirocentridae, a family of clupeiform fishes represented by the Recent wolf-herrings, *Chirocentrus,* have a long geologic history. Except for leptolepids, whose taxonomic allocation varies with different authors, chirocentrids are the earliest avowed teleostean family. Fifteen genera, nine of which are known from six or more specimens, are included in this family. Chirocentrids first appeared in the Jurassic and by the end of this period were represented by four genera. During the Cretaceous this family became further differentiated generically, and widely distributed. One Eocene genus perhaps belongs among the Chirocentridae. A single genus not known in the fossil record exists today, *Chirocentrus.* This family most closely resembles and probably shares a common ancestry with the Saurocephalidae. No teleostean family originated from the chirocentrids, whose origins appear to lie among the pholidophorids, rather than leptolepids as generally believed.

This study was undertaken to: (1) provide the first modern anatomical description and taxonomic revision of the living genus *Chirocentrus* and the fossil genera *Xiphactinus, Ichthyodectes* and *Gillicus*; (2) review taxonomically and, where possible, descriptively the 11 other genera of this family; (3) determine the phylogenetic history of the Chirocentridae; (4) compare the morphology of early clupeiform families and their holostean ancestors, and (5) discuss the origin and relationships of early Clupeiformes.

To assist the reader in following the comparisons and discussions presented hereafter, a brief statement on the groups concerned is necessary. Teleosts are derived from a single group of holosteans. Some ichthyologists separate this group from the holosteans as the superorder Halecostomi, which evolved in the early Mesozoic in the general direction of teleosts, while retaining a few of the more primitive holostean characters. The centra of the vertebrae are ringlike, perforated by the notochord. The vertebral column terminates in the base of the upper lobe of the caudal fin. The scales in some families, as Pholidophoridae, are rhomboid in shape and covered with a thin layer of ganoin, but in others, as Leptolepidae, they are thin, overlapping, and have little or no ganoin layer. Dermal bones of the upper jaw are slightly free, as in many teleosts. Teleostean ancestors are included in two families, Pholidophoridae and Leptolepidae.

The sequence pholidophorid-leptolepid-teleost, commonly accepted in the first 40-50 years of the 20th century, has been criticized (Saint-Seine, 1949; Gardiner, 1960; Nybelin, 1961; Schaeffer & Rosen, 1961) in recent years. The origin of leptolepids from pholidophorids was demonstrated by Rayner (1948), but it is the opinion of these authors that not all clupeiform fishes are derived from leptolepids. Instead, evolution of early clupeiforms progressed along at least two lines, one derived from pholidophorids, the other from leptolepids. Clupeids (herrings, sardines, Lower Cretaceous to Recent), clupavids (Upper Jurassic to Cretaceous), and the closely related dussumierids (Oligocene to Recent), are offshoots of leptolepids. Elopids (tarpon-type fishes, ?Late Jurassic to Recent), albulids (bonefishes, Upper Cretaceous to Recent), saurocephalids (slender, predatory fishes, Upper Cretaceous), pachyrhizodids (large, deep-bodied fishes, Upper Cretaceous), and probably several other families are derived from pholidophorids. Chirocentrids (wolf-herrings of today and their Cretaceous relatives) have been derived by most authors from leptolepids, but as shown in the section on "Evolution of Chirocentrid Fishes" I believe that they arose from pholidophorids.

Concerning my review of the chirocentrid genera other than *Chirocentrus, Xiphactinus, Ichthyodectes* and *Gillicus,* specimens of *Pachythrissops propterus, Proportheus kameruni, Prymnetes longiventer,* and *Eubiodectes libanicus* in United States museums were examined. The genera *Thrissops, Allothrissops, Mesoclupea, Spathodactylus, Chirocentrites, Cladocyclus,* and *Platinx* are reviewed by reference to literature. Jurassic species of *Thrissops* and *Allothrissops* were reexamined by Nybelin (1964). Chang (1963) reevaluated taxonomy and relationships of *Mesoclupea. Cladocyclus* was reviewed by Santos (1949, 1950). *Spathodactylus* and *Chirocentrites* were last studied by Woodward (1901) and *Platinx* by Eastman (1905). Although anatomy and taxonomy of all chirocentrid genera are not equally well known, a summary presentation of current knowledge is warranted because (1) this information is required for determination of chirocentrid history, and (2) scattered data on chirocentrids are brought together for the first time.

Several complete fishes, partial remains and isolated teeth have been referred erroneously to the Chirocentridae. Reasons for excluding these fishes are discussed in a separate section.

Analysis of neurocranial, jaw and scale structures suggests that two major radiations occurred in the history of chirocentrid fishes. The first took place in the Jurassic, resulting in the origin of *Thrissops, Allothrissops, Pachythrissops,* and *Mesoclupea.* The second radiation occurred in the Cretaceous and involved development of at least two principal branches from *Thrissops.* The first of these includes *Eubiodectes, Proportheus* and *Chirocentrus.* The second branch comprises *Spathodactylus, Prymnetes, Cladocyclus, Gillicus, Ichthyodectes, Chirocentrites,* and *Xiphactinus.*

PREVIOUS STUDIES

The family Chirocentridae was established by Cuvier & Valenciennes (1846) for the living species *Chirocentrus dorab* Cuvier (1817). In succeeding years, other species of *Chirocentrus* were described (see synonymy in Fowler, 1941).

During the first half of the 19th century several fossil teleosts characterized by laterally compressed, elongate bodies, dorsal and anal fins remote from snout, and enlarged dentition were discovered in England and Europe. Although such teleosts were compared with *Chirocentrus,* these fossils were not assigned to the Chirocentridae but referred to such diverse groups as halecoids, sphyraenoids (barracudas), sauroids, or clupeids (herrings). In the second half of the 19th century, North American fossil fishes now included in the Chirocentridae were classified as Saurodontidae Cope (1870), Saurocephalidae Zittel (1888), or Ichthyodectidae Crook (1892).

In the 20th century Chirocentridae were expanded to encompass fossil genera when Loomis (1900) and Woodward (1901) placed Ichthyodectidae in synonymy with Chirocentridae. Loomis and Woodward included *Saurodon* and *Saurocephalus* in the Chirocentridae, whereas Stewart (1899) placed these genera in a separate family, Saurodontidae. Berg (1940) segregated fossil from living forms under the names Ichthyodectidae and Chirocentridae, respectively, but included an Eocene genus, *Platinx,* in the Chirocentridae. *Thrissops,* for many years considered a leptolepid, was placed in the Chirocentridae by Saint-Seine (1945). This relationship had been suggested earlier by Heckel (1856) and Woodward (1895).

The family Chirocentridae, as interpreted in this paper, includes 15 genera, 10 of which were described in the 19th century and 5 in the 20th century. Prior to the 19th century, a specimen now assigned to *Allothrissops salmoneus* had been figured but not named (Knorr, 1755, pl. 31, fig. 1).

Anatomical studies of *Chirocentrus* have been confined chiefly to descriptions of head bones (RIDEWOOD, 1904b). Three fossil genera have been the object of several investigations: *Thrissops* (SAINT-SEINE, 1949, ARAMBOURG, 1954, NYBELIN, 1964), *Xiphactinus* (STEWART, 1900, LOOMIS, 1900, HAY 1898a) and *Ichthyodectes* (STEWART, 1900, LOOMIS, 1900). The other fossil genera have received little or no study subsequent to initial publication. Only one brief discussion (SAINT-SEINE, 1949) of chirocentrid phylogeny has appeared.

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METHODS AND TERMINOLOGY

Intensive description of three species, *Xiphactinus audax* LEIDY, *Ichthyodectes ctenodon* COPE, and *Gillicus arcuatus* (COPE) is founded on material in North American museums. Specimens of *Pachythrissops propterus, Proportheus kameruni, Prymnetes longiventer* and *Eubiodectes libanicus* were examined. Generic characteristics of *Thrissops, Spathodactylus, Chirocentrites*, and *Platinx* are summarized, using information derived from a comprehensive survey of literature on these chirocentrids and examination of specially requested photographs of holotypes of the type-species of these genera.

Five skulls of *Chirocentrus dorab* were cleared in sodium hydroxide or cleaned by hand. One skull was stained with alizarin to emphasize suture patterns. Evidence from dissection of *Chirocentrus dorab, Tarpon atlanticus*, and comparison with published accounts of neurocranial structure of Pholidophoriformes (RAYNER, 1948, GRIFFITH & PATTERSON, 1963), leptolepids (RAYNER, 1937), elopids (DUNKLE, 1940) and clupeids (TRACY, 1920) confirmed identification of nerve and blood vessel pathways in fossil chirocentrids.

With the following exceptions, nomenclature of skeletal elements follows that of NORDEN (1961): ethmoid (for hypethmoid and supraethmoid): parethmoid (for prefrontal) and intercalar (for opisthotic). Measurements and fin ray counts are made in the manner described by HUBBS & LAGLER (1958).

The following abbreviations for names of institutions are used.

Abbreviations for Names of Institutions

AMNH——American Museum of Natural History
BMNH——British Museum (Natural History)
CM——Carnegie Museum
CMNH——Cleveland Museum of Natural History
CNHM——Chicago Natural History Museum
DNHM——Denver Natural History Museum
FH——Fort Hays Kansas State College Museum
KU——University of Kansas Museum of Natural History
MCZ——Museum of Comparative Zoology, Harvard University
NMC——National Museum of Canada
OUSM——Oklahoma University Stovall Museum
SDSM——South Dakota School of Mines, Museum of Geology and Paleontology
SDNHM——San Diego Natural History Museum
TMM——Texas Memorial Museum
UNSM——University of Nebraska State Museum
USNM——United States National Museum
UT——University of Texas Bureau of Economic Geology
YPM——Peabody Museum, Yale University

GEOLOGIC AND GEOGRAPHIC DISTRIBUTION

Geologic history of chirocentrids extends from Middle Jurassic to Recent, a range which exceeds that of other teleostean families. Fossil chirocentrids are found on all continents. Geologic range and geographic distribution of fossil chirocentrid genera is summarized in Figure 1. Correlation of North American and Euro-

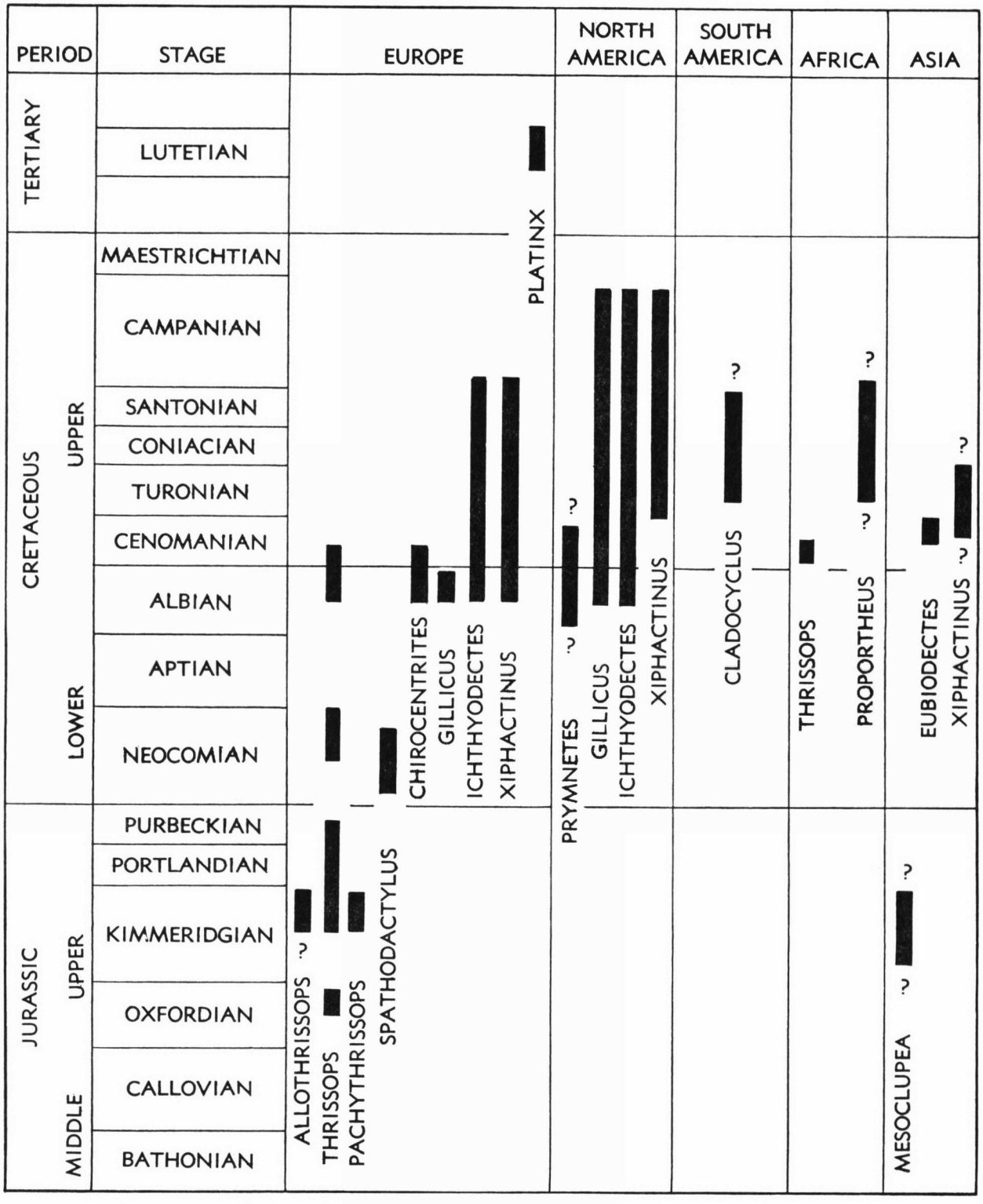


FIGURE 1. Geologic range and geographic distribution of fossil chirocentrid genera. Question marks indicate uncertainty in extent of geologic range or geologic position (see text).

pean stages is based on the works of IMLAY (1952) for the Jurassic; COBBAN & REESIDE (1952) and STEPHENSON *et al.* (1942) for the Cretaceous. Reasons for assigning fossil chirocentrids from other continents to a particular geologic horizon are given in this section. Question marks on Figure 1 indicate uncertainty of geologic position or geologic range of a particular genus. Geologic and general geographic distribution of each genus is discussed below. Specific localities from which specimens have been obtained are cited in the section on "Systematic Descriptions."

The first complete chirocentrids are known from the Kimmeridgian. Several pre-Kimmeridgian fish fragments originally described as species of *Leptolepis* have been referred to chirocentrids. NYBELIN (1964) tentatively assigned to *Allothrissops* one such pre-Kimmeridgian fragment, a preoperculum, from the Bathonian (Middle Jurassic) at Oxford, England. An incomplete fish from the Oxfordian at Christian Malford, England, was referred by WOODWARD (1895) to *Thrissops*. An undescribed fish collected by SCHAEFFER (personal communication) from the Sundance Formation (Upper Jurassic) in Wyoming is perhaps a *Thrissops*.

Specimens of several *Thrissops* species are abundant in Kimmeridgian deposits of the West German lithographic limestone quarries at Solnhofen, Eichstätt, and Kelheim, and in Kimmeridgian strata at Cerin, France. One specimen is recorded from equivalent beds in Dorsetshire, England. Other English fossils assigned to *Thrissops* have been found in Portlandian and Purebeckian strata on the Isle of Portland, Dorsetshire. A species from the lower Volgian (=Portlandian) of the Ulyanovsk district (USSR) is included questionably in this genus. *Thrissops* is known from the Neocomian at Tolfa and the Albian at Pietraroia, Italy. Several exposures of Cenomanian rock along the border between Italy and Yugoslavia, on the Isle of Lesina, and in equivalent strata at Jebel Tselfat in Morocco have yielded species of *Thrissops*. *Allothrissops* is known from Kimmeridgian beds at Solnhofen, Eichstätt, and Kelheim, West Germany, and Cerin, France. *Pachythrissops* is recorded only from the Kimmeridgian at Solnhofen and Eichstätt.

Specimens referred to *Mesoclupea* have been collected at several sites in Chekiang, Fukien, and Kiangsi Provinces in east central China. CHANG (1963) assigned the beds from which fishes of this genus were obtained to the Upper Jurassic on account of the close morphologic resemblances between *Mesoclupea* and European Upper Jurassic species of *Thrissops*. Unidentified "teleosts and ganoids" associated with *Mesoclupea* may give more concrete evidence of actual geologic position of these beds when these fishes are studied.

Chirocentrites is known from Albian (CITA, 1958) rocks at Pietraroia, Italy, and at Cenomanian localities in the Istrian karsts and on the Isle of Lesina. *Spathodactylus* is represented by a single specimen from the Neocomian Hivernage Limestone of Voirons, Switzerland. *Eubiodectes* is known only from the upper Cenomanian at Mt. Hakel and Mt. Hajula, Lebanon.

Proportheus occurs in the Late Cretaceous near Mamfe, Cameroun Republic, and at Ibando, Spanish Guinea. JAEKEL (1909), who first described this genus, believed it to be of Wealden age on the basis of comparison with *Thrissops* and *Portheus*. WEILER (1922) assigned fossils from Ibando to the Late Cretaceous for morphological rather than geologic reasons. ARAMBOURG & SCHNEEGANS (1936) assigned Ibando deposits to the late Albian or early Cenomanian and stated that fishes from Ibando were contemporaneous with those from the Istrian karsts and Lesina. The latter two European fish-bearing beds are of Cenomanian age. GÈZE (1943) concluded from study of lithology, paleobotany, and correlation with horizons of known age in neighboring regions that Mamfe fish deposits were referable to the Turonian-Senonian. He indicated that fossil-bearing layers at Ibando and Gabon (described by ARAMBOURG & SCHNEEGANS) were Turonian-Senonian. Further, ARAMBOURG & SCHNEEGANS noted many similarities between the Gabon fish assemblage and fossil fishes from Bahia and Riacho Doce in Brazil. These Brazilian deposits are considered Late Cretaceous (OLIVEIRA, 1956). In summary, *Proportheus* is a Late Cretaceous fish, probably from a stage younger than the Cenomanian deposits of Italy and Yugoslavia.

Cladocyclus occurs at three widely separated Brazilian localities. According to OLIVEIRA (1956), all of these sites are referable to the Upper Cretaceous but he does not correlate formations from which chirocentrid fossils were obtained with European stages. In Ceará, specimens referred to *Cladocyclus* have been found at Crato and Barra do Jardim in the Araripe Series (Santana Formation). In Bahia, specimens are recorded from localities surrounding the east coast of Todos os Santos Bay and on Itaparica Island. These sites are in the Bahia Series (Ilhas Formation). One species of *Cladocyclus* has been collected in Alagoas at Riacho Doce. This deposit is assigned to the Bahia Series.

The single specimen referred to *Prymnetes* was found near Tuxtla (presumably Tuxtla Gutierrez) in Chiapas, Mexico. The precise locality is unknown. MALDONADO-KOERDELL (1949) suggested a Senonian age. MASAROWITSCH (1958) stated that Lower and Upper Cretaceous, but primarily Upper Cretaceous (Cenomanian) rocks are present in Chiapas. DUNKLE (personal communication) suggests that this fish may have been found in an Eocene horizon.

Xiphactinus has the widest geographic distribution of all chirocentrids. In England, *Xiphactinus* first occurs in Albian strata and is last represented in the lower Senonian. Specimens referred to *Xiphactinus* are found in the upper Cenomanian (Zone of *Holaster subglobosus*) and in the Turonian (zones undetermined) of several English counties including Kent, Sussex, and Wiltshire. On the continent, *Xiphactinus* is found at Lezennes, France. These French fossils come from the upper Coniacian (Zone of *Micraster cortestudinarium*) according to SORNAY (1956). *Xiphactinus* also occurs in the Santonian (Craie phosphate) near Lonzée, Belgium. Specimens assigned to this genus have been collected in central Europe at several Cenomanian or Turonian localities (or both) near Prague, Czechoslovakia and near Strehlin, Poland.

The Australian species, *Xiphactinus australis*, was found near Hughenden, Queensland, in the Tambo Series (Rolling Downs Formation). DAVID (1950) correlated this series with the Albian of Europe but on the geologic map of Australia (dated 1931) included in his work, the Tambo Series is placed in the Upper Cretaceous. An Australian *Pachyrhizodus* (BARDACK, 1962) is also from this stratigraphic unit. In other parts of the world *Pachyrhizodus* is confined to the Upper Cretaceous. The present author is of the opinion that the Tambo Series is actually Upper rather than Lower Cretaceous.

In the United States *Xiphactinus* is represented at several stratigraphic levels from the Greenhorn Limestone (Cenomanian-Turonian) to the Selma Chalk (Campanian). Single specimens from Gorham and Holyrood, Kansas, were found in the Greenhorn Limestone. One specimen comes from the Carlile Shale near Fairbury, Nebraska. HILL (1901) has mentioned vertebrae of *Xiphactinus* obtained from the Eagle Ford Shale close to the contact of this shale with the Austin Chalk on the Bosque River near Waco, Texas. Numerous specimens assigned to *Xiphactinus, Ichthyodectes*, and *Gillicus* are found in the Smoky Hill Chalk Member of the Niobrara Formation. Few, if any, specimens of these fishes have been obtained from the underlying Fort Hays Limestone Member. Exact localities for most fossil vertebrates from the Niobrara Formation are unknown. *Xiphactinus* specimens are recorded from the Austin Chalk near Britton, Celina, and Savoy, Texas, the Selma Chalk of Dallas, Greene, and Hale counties, Alabama, and Sevier County, Arkansas. STEPHENSON (1912) listed *Xiphactinus* teeth from Sampson, Greene, and Lenoir counties, North Carolina. These fossils come from the Snow Hill Marl Member of the Black Creek Formation, which is correlated with lower and middle beds of Pierre Shale.

In Canada, *Xiphactinus* has been found in the Upper Cretaceous Vermilion River Formation near Altona, Manitoba, and in an undetermined formation east of Lesser Slave Lake, Alberta (LANGSTON, personal communication). The latter locality represents the northernmost record of this genus. A scale referred to *Xiphactinus* sp. by MALDONADO-KOERDELL (1956) from the Agua Nuevo Formation (upper Turonian) at Xilitla, San Luis Potosi, Mexico, is too fragmentary for positive assignment to this genus.

Ichthyodectes is confined almost entirely to the Upper Cretaceous. One specimen (WOODWARD, 1901), was found in the English Albian at Folkestone, Kent. Specimens of *Ichthyodectes* have been collected in the English Chalk at several upper Cenomanian (Zone of *Holaster subglobosus*) and Turonian (zones undetermined) localities in Kent, Surrey, and Sussex. Scales of *Ichthyodectes* are reported from the Senonian near Anzin and Lezennes, Frances (LERICHE, 1902).

An isolated scale (REESIDE, 1923) from the South Platte Formation (WAAGE & EICHER, 1960) near Bellevue, Colorado, probably belongs to *Ichthyodectes*. If correctly identified, this scale represents the earliest record of *Ichthyodectes* in the United States. *Ichthyodectes* vertebrae (ZANGERL & SLOAN, 1960) have been found in the Carlile Shale (probably Turonian) near Milbank, Grant County, South Dakota. SLOAN has shown me more complete, but still unprepared specimens of *Ichthyodectes* from an adjacent locality of the same strata. *Ichthyodectes* is abundantly represented in the Niobrara Formation of western Kansas. One specimen has been collected from the Selma Chalk in Greene County, Alabama. The Selma Chalk is correlated with middle beds of the Pierre Shale (ZANGERL, 1948). Specimens assignable to *Ichthyodectes* come from the Sharon Springs Member of the Pierre Shale northeast of Red Bird, Wyoming, and near Fairburn

and Edgemont, South Dakota. Part of a vertebral column from the Agua Nueva Formation (upper Turonian) at Xilitla, San Luis Potosi, Mexico, was referred to *Ichthyodectes* sp. by MALDONADO-KOERDELL (1956).

In Europe, *Gillicus* is represented only at the top of the Lower Cretaceous from Albian beds in Kent, England. In the United States an isolated scale (*Hypsodon? granulosus* COCKERELL, 1919) which may belong to this genus is known from the Mowry Shale near North Rawlins, Wyoming. More positively identifiable scales and other structures of *Gillicus* are included in the material which SLOAN has shown me from the Carlile Shale at Milbank, Grant County, South Dakota, and the Niobrara Formation of Lac Qui Parle County, Minnesota. Numerous specimens referable to *Gillicus* have been collected in the Niobrara Formation of western Kansas. Scales and vertebrae pertaining to this genus are known from the Austin Chalk. Several sites in Manitoba, Canada, have yielded *Gillicus* scales. *Gillicus* is last recognized from the Sharon Springs Member of the Pierre Shale northeast of Red Bird, Wyoming.

Platinx is known from the Lutetian (middle Eocene) at Monte Bolca, near Verona, Italy.

Chirocentrus occurs on the east coast of Africa in the vicinity of Natal north to the Red Sea, across the Indian Ocean to Indonesia and several Melanesian islands, south to Queensland, Australia, and north through the Philippines and Taiwan to Japan. There is no fossil record of *Chirocentrus*.

ENVIRONMENTAL CONDITIONS AND PRESERVATION OF SPECIMENS

Chirocentrids were inhabitants of shallow seas, coastal waters, estuaries, and lagoons, as indicated by organisms associated with these fossils. Associated organisms include foraminifers, corals, brachiopods, mollusks, sharks, rays, and numerous kinds of bony fishes. Lithology and ecological conditions of localities yielding remains of chirocentrids are reviewed below.

Thrissops and *Allothrissops* are common at Cerin, France, in a channel deposit formed in calm sea water on the coastal side of a barrier reef (SAINT-SEINE, 1949). The lithographic limestones of Bavaria from which species of *Allothrissops, Thrissops,* and *Pachythrissops* have been obtained are the product of marine sedimentation and represent deposits in a shallow lagoon (ARKELL, 1956). Ecologic conditions of the Jurassic, Portlandian, and Purbeckian beds of southern England have been reviewed by RAYNER (1958).

According to CHANG (1963), *Mesoclupea* is from "fluvial-lacustrine deposits with *Sinamia* sp., teleosts, and a great number of fresh-water shells and conchostracans." If this environment is correctly evaluated, *Mesoclupea* is the only chirocentrid recorded from fresh water. Whether *Mesoclupea* was restricted to fresh water or ascended rivers seasonally cannot be determined.

Xiphactinus, Ichthyodectes, and *Gillicus* from Albian, Cenomanian, Turonian, and Senonian deposits of England are found in glauconitic sands, chalky marls, and argillaceous chalk. LADD (1957) stated that the depth of the seas which formed the English Chalk ranged from less than 50 to about 300 fathoms. The few Upper Cretaceous specimens of *Xiphactinus* and *Ichthyodectes* from northern Europe are found in chalk deposits which, in view of associated invertebrates, suggest ecologic conditions resembling those of the English Chalk.

Spathodactylus comes from richly fossiliferous glauconitic or phosphatic beds described by GIGNOUX (1950) as shallow-water deposits. Specimens of *Thrissops* and *Chirocentrites* from the Albian of Italy occur in a compact, gray, flinty, silicaceous rock (CITA, 1958).

Upper Cretaceous *Thrissops* and *Chirocentrites* specimens from Italy and Yugoslavia occur in black calcareous schists and slates of bituminous schists (CITA, 1958). According to ERASMO (1946), these marine sediments were deposited in a warm-water gulf not far from the coast. The Eocene calcareous shales of Monte Bolca containing *Platinx* represent a shallow marine facies (GIGNOUX, 1950).

WEILER (1922) stated that *Chirocentrites? guinensis* (in this study *Proportheus kameruni*) died in the foul bottom waters of a brackish lagoon into which it pursued its prey. These deposits were described as sublittoral by FURON (1960). *Thrissops* specimens from Jebel Tselfat (ARAMBOURG, 1954) are found in a black bituminous deposit into which these fishes were transported after death.

Fossils of *Cladocyclus* from Riacho Doce occur in a bituminous shale probably of estuarine origin (DERBY, 1907). The Bahia fossil-bearing layers containing species of *Cladocyclus* are composed of green-olive, calcareous concretions. These sediments (ERASMO, 1938), formed near the mouth of a river, were of marine origin.

Ichthyodectes specimens from Milbank, South Dakota, occur in an arkosic, chalky marl deposited on a boulder beach (ZANGERL & SLOAN, 1960). Niobrara

Formation chirocentrids *Xiphactinus, Ichthyodectes,* and *Gillicus* come from gray chalk and calcareous shales colored by an accumulation of organic material. These sediments were formed in a relatively calm, densely stratified, epicontinental sea (MILLER, 1958, unpublished Ph.D. thesis, University of Kansas). REESIDE (1957) stated that Niobrara faunas lived in shallow, relatively quiet water. REESIDE considered that the Austin Chalk, in which these genera also occur, closely resembles the Niobrara Formation [See ZANGERL (1948) regarding ecological conditions of the Selma Chalk which has yielded specimens of *Ichthyodectes* and *Xiphactinus.*] Specimens of *Ichthyodectes* and *Gillicus* from the Pierre Shale are contained in black sands, muds and shales. These sediments were laid down in calm water, not far from coastal areas of low relief (REESIDE, 1957).

Chirocentrus is a coastal, pelagic fish. HARDENBERG (1930) thought that one species lives "near" the coast and the other "far" from the coast. In summary, evidence presented by authors who have studied lithology and associated faunas of the numerous localities yielding chirocentrids indicates that these fishes were and still are inhabitants of a warm-water, pelagic, euryhaline environment.

At least one entire, intact or nearly complete specimen representing each fossil chirocentrid genus is known, with the exception of *Eubiodectes.* The numerous, complete chirocentrid specimens from the Jurassic lithographic limestones, generally preserved as part and counterpart, show well-preserved postcranial structures but cranial structures are crushed.

Chirocentrids from the Cretaceous black bituminous schists of Italy and Yugoslavia are less abundant than those from the Jurassic limestones and few complete specimens have been found. The condition of chirocentrids known from single individuals or at isolated localities is indicated in the "Systematic Descriptions" section.

The majority of chirocentrid specimens from the English Chalk consist of isolated jaws, vertebrae, and scales. Heads of few individuals are known. Of chirocentrid genera common to the English Chalk and Niobrara Formation, specimens from the former appear to be consistently smaller than those from the latter, to judge from data in WOODWARD (1903, 1907) and my examination of Niobrara specimens.

Several complete, intact chirocentrid skeletons have been collected from the Niobrara Formation. Specimens of the larger fish *Xiphactinus audax* are more abundant than the smaller *Ichthyodectes ctenodon* or *Gillicus arcuatus.* Twenty more or less complete specimens referable to the first genus, but only four of the other two combined are known. Approximately three-fifths of the chirocentrids from Cretaceous deposits in the United States are referable to *Xiphactinus,* almost one-fifth to *Gillicus* and one-fifth to *Ichthyodectes.* Chirocentrids comprise slightly more than two-fifths of the total Niobrara Formation fish assemblage.

Several of the complete *Xiphactinus audax* specimens show remains of undigested prey within the abdominal cavity. The excellently preserved *Xiphactinus* (FH no. 5026) contains the most complete example of *Gillicus arcuatus.* One *Xiphactinus audax* specimen includes a fragmentary *Ananogmius* sp. within its abdominal cavity; another has several shark teeth. Complete specimens of *Xiphactinus audax* and the stomach contents of each are listed in Table 3 accompanying the description of this species.

HARDENBERG (1930) mentioned a specimen of *Chirocentrus dorab* which contained within the abdominal cavity another *Chirocentrus dorab.* The prey, one-third the size of the predator, was merely engulfed. There was no indication that the enlarged teeth characteristic of these fishes had been used to slash or cut the smaller fish. The essentially undisturbed skeleton of *Gillicus* within the Fort Hays *Xiphactinus* suggests that the feeding process of Cretaceous chirocentrids was similar to that of the living genus.

A specimen of *Thrissops formosus* from the West German lithographic limestone contains small fishes which NEUMAYER (1929) thought were young of this species. He concluded that these small fishes were located in the oviduct above the alimentary tract and that *Thrissops* thus was viviparous. NYBELIN (1958) demonstrated that these small fishes were not young *Thrissops,* but probably leptolepids which actually were enclosed in the stomach. He suggested that *Thrissops* was a rapid swimmer preying seasonally on pelagic plankton or small, schooling leptolepid fishes. Development of viviparity among isospondyls, especially in but one genus of a family, would be unusual.

EVOLUTION OF CHIROCENTRID FISHES

The Chirocentridae are one of six living clupeiform families (ROMER, 1945) with a pre-Tertiary fossil record. Only chirocentrids, at the present time, are recognized from the Jurassic. The five other families, Elopidae, Albulidae, Pterothrissidae (deep-sea bonefishes), Clupeidae, and Chanidae, are first recorded in the Cretaceous. An attempt to trace ancestral-descendant relationships within a single family of early teleosts has been made only for the Chirocentridae (SAINT-SEINE, 1949). Analysis of chirocentrid evolutionary history is possible because (1) this family forms a distinct unit of phyletically related fishes, whereas elopids and clupeids as usually defined represent an association of several morphologically distinct groups, (2) the chirocentrid fossil record includes more kinds and better-preserved fishes than those of the other families, especially Albulidae, Pterothrissidae, and Chanidae, and (3) anatomy of many chirocentrid genera, including earliest and latest members, has received more intensive study relative to genera of the five other families. In this section, evolution within the Chirocentridae and origin of this family will be discussed.

The outline of chirocentrid phylogeny developed by SAINT-SEINE is presented in Fig. 2. He examined only Jurassic species of *Thrissops* from France. The remainder of his reconstruction was founded on an incomplete survey of literature on chirocentrids. Expanded knowledge of chirocentrid anatomy obtained in the present study requires several alterations in ancestral-descendant relationships as depicted by SAINT-

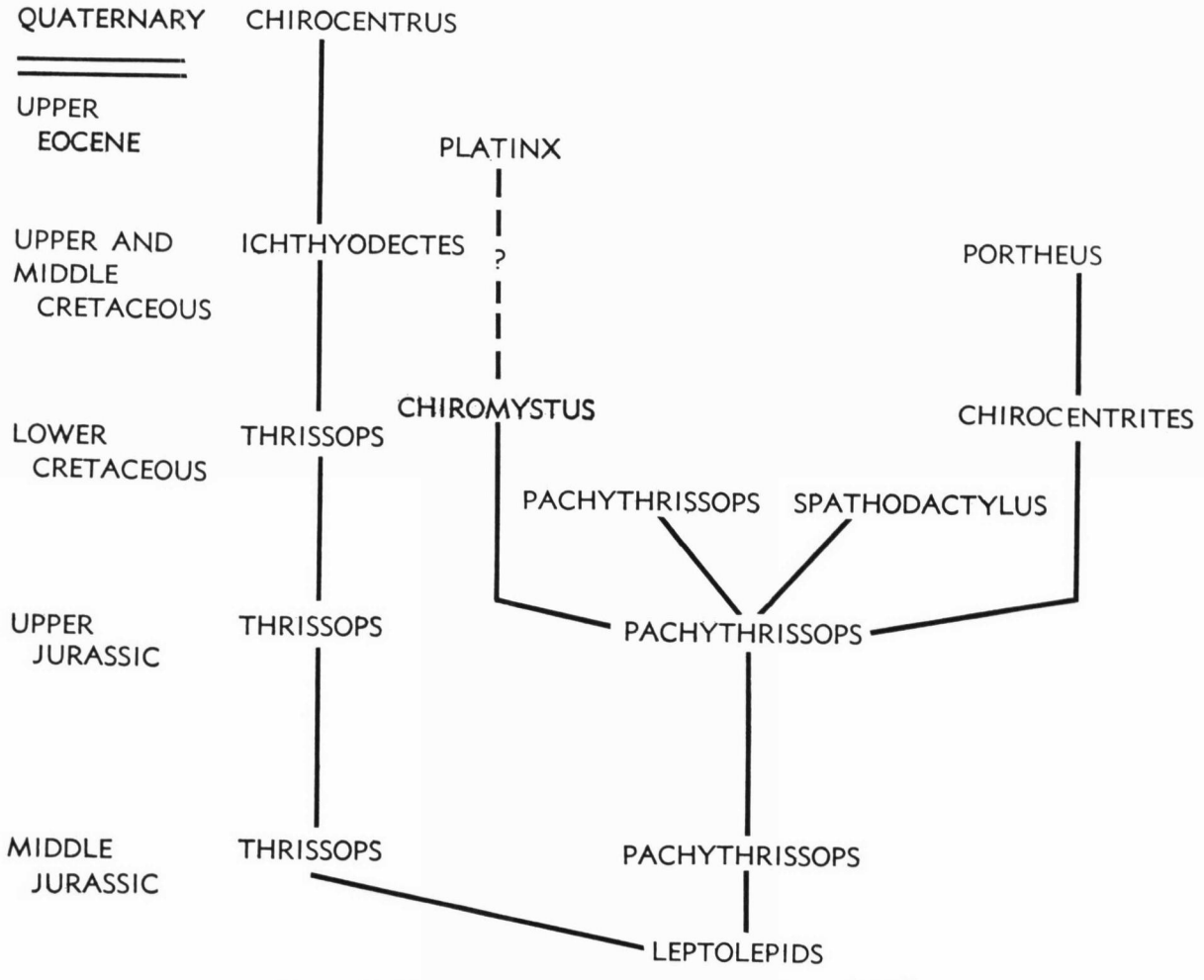


FIGURE 2. Chirocentrid phylogeny after SAINT-SEINE (1949).

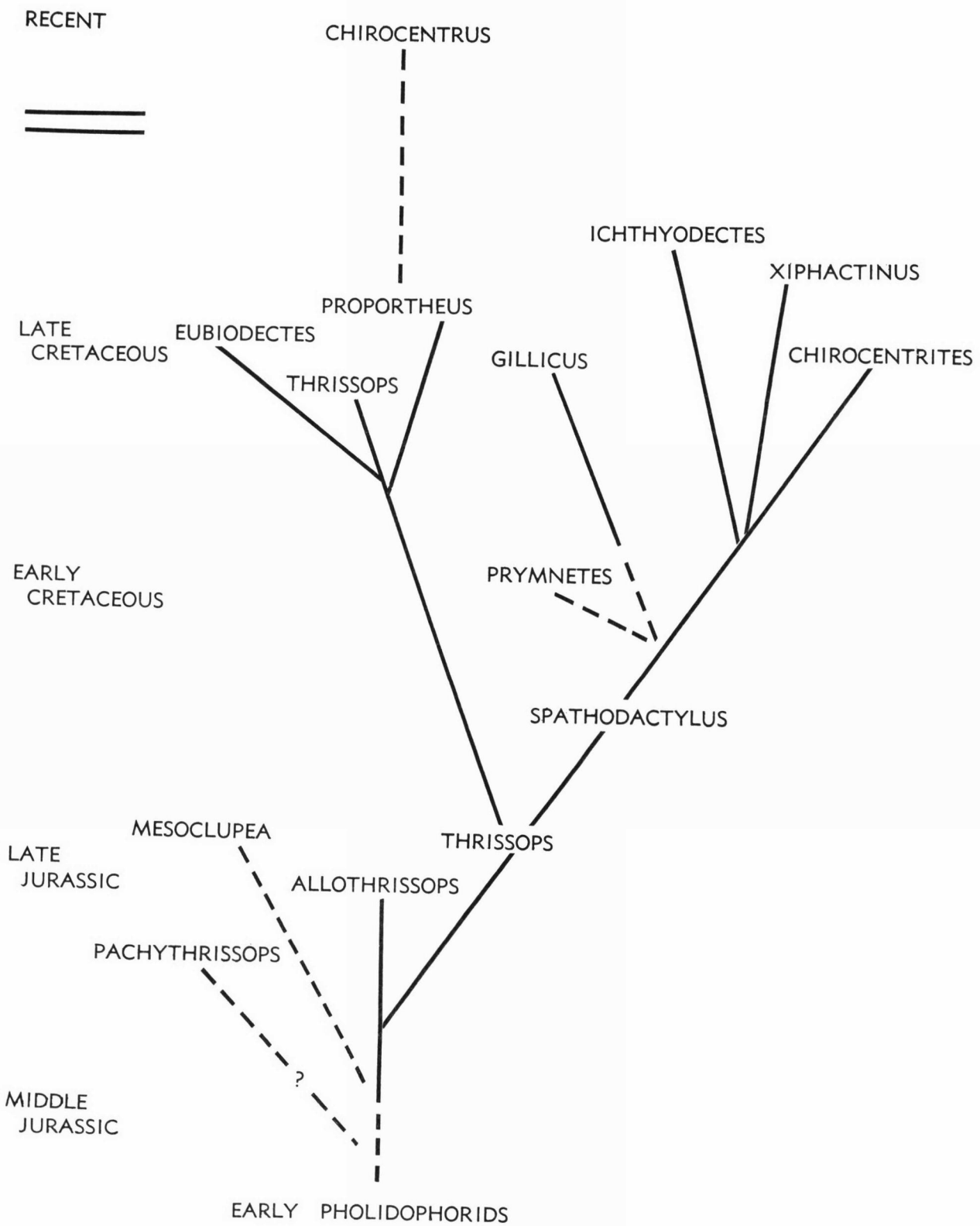


FIGURE 3. Proposed relationships of chirocentrid fishes.

SEINE. Six genera, *Gillicus, Proportheus, Prymnetes, Eubiodectes, Mesoclupea,* and *Allothrissops,* the first four of which were included in the Chirocentridae at the time SAINT-SEINE published, are added to the revised phylogeny (Fig. 3). One genus, *Platinx*, is not shown in the revised phylogeny because association of this fish with the Chirocentridae is uncertain.

In theory, phylogeny is deduced by tracing changes in a series of structures from geologically earlier to later members of a family. Because of existing limitations in the teleostean fossil record, brief comment on the nature and reconstruction of ancestral-descendant relationships of a teleostean family is necessary. The teleostean fossil record is discontinuous; fossils of one family are frequently limited to only one or two stratigraphic horizons. Incomplete preservation of specimens is a common occurrence. In many cases, fossils of one family are nearly or actually taxonomically identical (at the generic level) with living members of that family. Taxa anatomically and geologically intermediate between earlier and later forms are usually unknown. As a result of these limiting factors, a phylogeny (perhaps more properly termed a dendrogram) even of those few teleostean families with a reasonably adequate fossil record is, to a large degree, based on morphological similarities and differences. Such a phylogeny represents an association of morphologic stages. Structures selected to trace changes from stage to stage should include:

(1) Those of the adaptive morphologic complex of a particular family. Changes traced in such a suite of intimately related structures rather than in a group of randomly selected structures of independent origin should reduce the chance that unrelated fishes might be united in a phylogeny. A phylogeny deduced from randomly selected structures could be erroneous because convergent development of analogous anatomical features in distinct lineages is a common phenomenon of teleostean evolution.

(2) A series of structures which may be traced from primitive to advanced stages. The primitive condition should be substantiated by (a) initial appearance in geologically oldest taxon, (b) widespread occurrence in early teleosts, (c) observation of changes in the appearance of a given structure in the course of time.

In addition, minor structural similarities whose evolutionary history is not completely known at present, can be useful for tracing relationships between geologically contemporaneous taxa.

The following are characters of the chirocentrid morphologic complex.

(1) Body elongate, slender and laterally compressed.
(2) Snout fully ossified.
(3) Supraoccipital crest prominent.
(4) Dorsolateral neurocranial ridge formed by parietal and epiotic.
(5) Ventral end of parethmoid with enlarged, swollen head.
(6) Post-temporal fossa or groove developed.
(7) Mouth cleft directed upward.
(8) Quadrate-mandibular joint below middle or anterior end of orbit.
(9) Premaxillary and maxillary firmly united.
(10) Single row of conical teeth in alveoli on all jaws.
(11) Centra with stout, longitudinal, lateral ridge.
(12) Dorsal and anal fins remote from snout.
(13) First pectoral fin ray broad and spinose.

Development of these characters varies in individual genera or species. For example, the body of *Thrissops subovatus* is relatively deeper than in other chirocentrids. *Mesoclupea* lacks an epioticoparietal ridge. The supraoccipital crest of *Chirocentrus* and *Mesoclupea* is lower than in other genera.

The anatomy of *Allothrissops, Thrissops,* and *Mesoclupea* provides evidence of the primitive chirocentrid condition. Primitive and advanced characters of the chirocentrids are listed in Table 1. Because anatomical knowledge of geologically early chirocentrids is incomplete, it is necessary to explain how the primitive condition of several characters is determined. The nature of morphologic change in several characters also requires clarification. The numerical sequence below corresponds to that of the primitive and advanced characters cited in Table 1.

(1) An absolute increase in body length occurs in most but not all genera in the course of chirocentrid evolution. The proportion of head length to standard length is also changed. Thus, in Jurassic chirocentrids this ratio varies from 4.25-5 *(Allothrissops regleyi)* to 5.7-6.7 *(Thrissops formosus)*. In Cretaceous genera this ratio ranges from 5.5-6 *(Xiphactinus audax)* to 6.5-7 *(Ichthyodectes ctenodon* and *Thrissops vexillifer)*.
(2) The supraoccipital crest increases from approximately 0.25 *(Allothrissops)* to 0.33 *(Xiphactinus)* or 0.5 *(Gillicus)* the posterior neurocranial height.
(3) No comment necessary.
(4) In *Allothrissops* and other early teleosts in which parethmoid shape is known, the palatine head of this bone extends anteriorly below the nasal capsule and the articular facet which receives the palatine lies at the anteroventral end of this bone. In *Chirocentrus*, the malleolar head does not project below the nasal capsule and the articular facet is directed ventrolaterally.
(5) A mid-sagittal, vertical process of the basisphenoid probably is present in early chirocentrids, because such a process exists in families from which teleosts are derived (leptolepids and pholidophorids), elopids, and several Cretaceous chirocentrids.

TABLE 1. *Primitive and Advanced Characters of Chirocentrids.*

PRIMITIVE	ADVANCED
1. Body generally 1 m. or less in length.	1. Body generally 1 m. or more in length.
2. Supraoccipital crest low.	2. Supraoccipital crest enlarged.
3. Parietals joined at mid-sagittal line.	3. Parietals separated by supraoccipital at mid-sagittal line.
4. Palatine head of parethmoid directed ventroanteriorly.	4. Palatine head of parethmoid directed ventrolaterally.
5. Basisphenoid with ventral process.	5. Basisphenoid without ventral process.
6. Intercalar small.	6. Intercalar enlarged.
7. Subtemporal fossa present.	7. Subtemporal fossa absent.
8. Post-temporal fossa present.	8. Post-temporal groove present.
9. Basipterygoid process present.	9. Basipterygoid process absent.
10. Auditory fenestra absent.	10. Auditory fenestra present.
11. Temporal foramen absent.	11. Temporal foramen present.
12. Several foramina open into trigeminofacial chamber.	12. Single, large foramen opens into trigeminofacial chamber.
13. Oculomotor nerve emerges through prootic.	13. Oculomotor nerve emerges through basisphenoid.
14. Mouth cleft opens slightly above terminal position.	14. Mouth cleft angled sharply upward from horizontal axis.
15. Premaxillary with ventroposterior process.	15. Premaxillary without ventroposterior process.
16. Low-crowned dentition of uniform or nearly uniform size.	16. High-crowned dentition generally of irregular size.
17. Coronoid process rises more or less sharply above dental border. This process is prolonged posteriorly in a horizontal line.	17. Coronoid process short. Profile of mandible drops sharply toward quadrate-mandibular articulation.
18. Longitudinal lateral ridge of centra slightly developed. Centra frequently exhibit secondary longitudinal ridges.	18. Longitudinal, lateral ridge of centra enlarged.
19. Anal fin of more than 20 rays.	19. Anal fin of less than 20 rays.
20. Scales usually with circuli only.	20. Scales with anterior radii and posterior punctae.

(6) The intercalar of most early teleostean families is a small bone restricted to posterior and lateral surfaces of the neurocranium. Such is the case in *Chirocentrus*. The intercalar of the *Xiphactinus* group of chirocentrids is expanded especially on the lateral neurocranial surface in such a way that part of the hyomandibular fossa, normally entirely incised in replacement bone, extends into this dermal bone. This expansion provides increased area for support of the enlarged hyopalatine arch.

(7) A subtemporal fossa is presumed to be present in early chirocentrids for the same reasons as those cited for character 5.

(8) A post-temporal fossa is developed in leptolepids and pholidophorids, as well as Mesozoic chirocentrids. In *Chirocentrus*, erosion of the pterotic-parietal roof transforms this fossa into a groove.

(9) A basipterygoid process must be present in early chirocentrids for the same reasons cited to establish the primitive condition of character 5.

(10) An auditory fenestra is not present in leptolepids, pholidophorids or Mesozoic teleosts. This fenestra appears in *Chirocentrus* and several living clupeoids.

(11) A temporal foramen is not developed in leptolepids, pholidophorids or Mesozoic teleosts. This foramen appears in *Chirocentrus* and several living clupeoids.

(12) Several foramina enter the trigeminofacial chamber in leptolepids, Cretaceous chirocentrids and other Cretaceous teleosts. Therefore, multiple foramina are considered the primitive condition in contrast to the single large opening in *Chirocentrus* and many living Clupeiformes.

(13) Primitive position of the oculomotor nerve is established for the same reasons as the primitive condition of character 12.

(14) In Jurassic chirocentrids the quadrate-mandibular articulation lies below the middle of the orbit. This articulation moves anteriorly, especially in *Thrissops vexillifer*, but also in other Cretaceous chirocentrids.

(15) One group of chirocentrids has lost the ventroposterior process of the premaxillary, as well as a bony connection between premaxillary and ethmoid. This ventroposterior process is retained in most families of early teleosts and in *Chirocentrus*.

(16) In the primitive stage, dentition is of uniform size and teeth probably arise from shallow alveoli. However, we have no direct statement on the presence or absence of alveoli from authors who have studied Jurassic chirocentrids. Later chirocentrids (including the Jurassic species *Thrissops subovatus*) have enlarged teeth in deep or shallow alveoli. In some genera only a few teeth or teeth of only one jaw are enlarged.

(17) In pholidophorids and especially leptolepids the coronoid process rises more or less sharply above the dental border of the mandible. This process is elongate and its dorsal border essentially parallel to the ventral border of the mandible. Early chirocentrids such as *Allothrissops* show an enlargement of the coronoid process relative to that of later chirocentrids, such as *Thrissops* and *Ichthyodectes*. The coronoid process of later genera is short and only slightly higher than the posterior end of the mandibular alveolar border. Behind this process the dorsal mandibular margin drops sharply to the quadrate-mandibular articulation.

(18) No comment necessary.

(19) No comment necessary.

(20) Scales of the Cretaceous *Thrissops vexillifer* show a few anterior radii but none appear in Jurassic *T. formosus* or *Mesoclupea*. Radii and punctae are otherwise an exclusive feature of the *Xiphactinus* group of chirocentrids.

RADIATION OF CHIROCENTRIDAE

Two principal periods of origin and diversification are recognized in the evolutionary history of this family. During the initial period (Middle Jurassic-Late Jurassic), four genera, *Allothrissops, Thrissops, Mesoclupea,* and *Pachythrissops* evolved. These genera exhibit the suite of primitive characters listed in Table 1. *Thrissops* has developed several advanced characters. For example, (1) the mouth cleft is angled sharply upward as in Cretaceous chirocentrids, (2) dentition is enlarged and of irregular size, (3) the coronoid process is not enlarged as in *Allothrissops*, and (4) a single, longitudinal lateral ridge is developed on the centra.

The second period of chirocentrid radiation took place in the Cretaceous from *Thrissops*. Ten genera of wide geographic distribution resulted from this radiation. These ten genera developed along two phyletic lines. The first line includes Cretaceous species of *Thrissops, Eubiodectes, Proportheus*, and the Recent *Chirocentrus*. For convenience these genera are collectively referred to as the *Chirocentrus* group. The second line includes *Spathodactylus, Prymnetes, Gillicus, Cladocyclus, Ichthyodectes, Chirocentrites*, and *Xiphactinus*. For convenience these genera are referred to in this discussion as the *Xiphactinus* group. Establishment of these two groups is supported by geographic distribution as well as morphology. The *Chirocentrus* group includes European, African, and Asian fishes. The *Xiphactinus* group comprises European, Asian, North and South American fishes.

Mesozoic members of the *Chirocentrus* group retain most of the primitive chirocentrid characters but *Chirocentrus* has developed many advanced characters. In the Cretaceous species, *Thrissops vexillifer*, the advanced condition of characters 3 (parietals separated at midsagittal line), 14 (mouth cleft angled sharply upward) and 18 (longitudinal, lateral ridge of centra enlarged) is recognized.

Chirocentrus exhibits an advanced condition of characters 3 (parietals separated at mid-sagittal line), 4 (palatine head of parethmoid directed ventrolaterally), 5 (basisphenoid without a ventral process), 7 (subtemporal fossa absent), 8 (post-temporal groove present), 9 (basipterygoid process absent), 10 (auditory fenestra present), 11 (temporal foramen present), 12 (single, large foramen opens into trigeminofacial chamber), 13 (oculomotor nerve emerges through basisphenoid), 14 (mouth cleft angled sharply upward), 16 (high-crowned dentition), 17 (coronoid process low and short), 18 (longitudinal lateral ridge of centra enlarged).

Characteristics of the *Xiphactinus* group will be cited as a unit rather than specified for individual genera because genera of this group are (a) essentially uniform in structure with regard to the 20 primitive and advanced characters, (b) limited to the Cretaceous (primarily the Late Cretaceous). In addition, anatomy of the earliest genus of this group, *Spathodactylus*, which should show important transitional features is inadequately known. Characteristics of the *Xiphactinus* group are (1) body generally above 1 m. in length, (2) supraoccipital crest enlarged, (3) parietals joined at mid-sagittal line, (4) palatine head of parethmoid projected anteroventrally below nasal capsule, (5) basisphenoid with ventral process, (6) intercalar enlarged, (7) subtemporal fossa present, (8) post-temporal fossa present, (9) basipterygoid process present, (10) auditory fenestra absent, (11) temporal foramen absent, (12) several foramina opening into trigeminofacial chamber, (13) oculomotor nerve emerging through prootic, (14) mouth cleft angled sharply upward from horizontal axis, (15) premaxillary without ventroposterior process, (16) dentition enlarged and of uniform or irregular size, (17) coronoid process short, low, and dorsal profile of mandible dropping sharply toward quadrate-mandibular joint, (18) longitudinal, lateral ridge of centra enlarged, (19) anal fin of less than 20 rays, (20) enlarged scales with radii and punctae. The *Xiphactinus* group thus exhibits 10 characters (nos. 1, 2, 6, 14, 15, 16, 17, 18, 19, 20) in an advanced stage of development.

PHYLOGENETIC CONNECTIONS AMONG GENERA

In discussion below, ancestral-descendant relationships among chirocentrid genera are indicated and morphologic changes in genera with long geologic ranges are noted. Relationships among Jurassic genera are considered first, followed by the *Chirocentrus* group and finally the *Xiphactinus* group.

Allothrissops, a genus recently established (Nybelin, 1964) to accommodate three species formerly included in *Thrissops*, is known from the Kimmeridgian (Late Jurassic) and perhaps even from the Bathonian (Middle Jurassic). Nybelin has cited a preoperculum from Bathonian deposits near Oxford, England, which resembles that of *Allothrissops*. Superficial cranial anatomy of *Allothrissops* has been illus-

trated by SAINT-SEINE (1949, fig. 116). This genus shows the suite of characters designated as primitive for this family.

Sensory canal development is more primitive than in other chirocentrids. According to SAINT-SEINE, *Allothrissops* sensory canals exhibit a teleostean pattern but retain vestiges of the parietal pit-lines of nonteleostean actinopterygians. Anterior and median pit-lines on each parietal no longer connect with the supraorbital sensory canal commissure, as they do in *Pholidophorus* or *Leptolepis*, for example. These pit-lines form a narrow, deep furrow. The supraorbital canal develops a connection with both cephalic sensory canal and circumorbital sensory canal by way of a pterotic canal. The frontal bones of *Allothrissops* lose the relatively planar surface of preteleosteans and develop a longitudinal furrow in which the supraorbital sensory canal lies. Extensive preopercular and circumorbital sensory canals are present.

Allothrissops and *Thrissops* are closely related (NYBELIN, 1964) but the former retains all primitive chirocentrid characters, especially a sharply raised, elongate coronoid process and minute dentition on all jaws. *Allothrissops* is considered the stem chirocentrid genus.

Thrissops was for many years (WOODWARD, 1895; ROMER, 1945) included among the leptolepids. SAINT-SEINE (1949) removed *Thrissops* from the leptolepids and placed it among the chirocentrids, principally for reasons which differentiate halecostomes, as represented by leptolepids, from teleosts. These reasons include (1) formation of crests and furrows on the cranial roof with emphasis on supraoccipital crest, (2) otic region of neurocranium enlarged and projecting laterally, (3) sphenotic process enlarged, (4) parethmoid head enlarged, and (5) supraorbital sensory canal connected to lateral line.

A species of *Thrissops (T. costalis)* is recorded from the Oxfordian (Late Jurassic). *Thrissops* last appeared in the Late Cretaceous. Although the geologic record of *Thrissops* is not continuous in this interval, it has the longest geologic range of any chirocentrid.

In the course of its history, the body of *Thrissops* became longer and more slender. The head is included ?5-6.75 times in the standard length of Jurassic species and 6-7 times in Cretaceous species. The supraoccipital, initially separated from frontals by midsagittally united parietals, separates the parietals in the single Cretaceous species *(T. vexillifer)* in which the relationship of these bones has been described. Whether parietals reach the posterior end of the neurocranium (ARAMBOURG, 1954, fig. 23) in *T. vexillifer* requires reinvestigation. The epiotic of other Cretaceous chirocentrids expands medially to meet the supraoccipital, whereas parietals are reduced and confined to the dorsal surface of the neurocranium. The structure of the lateral neurocranial wall of a Jurassic chirocentrid is unknown. The quadrate-mandibular joint lies below the middle of the orbit in Jurassic species and below the anterior end of the orbit *(Thrissops microdon)* or below the snout *(T. vexillifer)* in Cretaceous species.

In comparison with other Jurassic chirocentrids, *Thrissops* exhibits (1) a straight maxillary dental border, (2) a low coronoid process not enlarged as in *Allothrissops*, and (3) dentition enlarged and of irregular size (especially in *T. subovatus*). These characters foreshadow morphologic developments in later Mesozoic chirocentrids. NYBELIN does not believe that any of the three species of *Allothrissops* is the direct ancestor of any species of *Thrissops*. However, the morphology of these two genera is sufficiently alike to permit a suggestion that these fishes share a common ancestry.

The primitive condition of *Mesoclupea* is demonstrated by (1) a blunt snout unlike the more pointed snout of chirocentrids but similar to that of leptolepids, (2) flat cranial roof, (3) "very small" supraoccipital crest (CHANG, 1963), (4) parietals united along almost their entire medial border, (5) palatine head of parethmoid directed vertically rather than ventroanteriorly, (6) mouth cleft nearly terminal, (7) centra with several fine longitudinal lateral ridges. In contrast with *Allothrissops, Mesoclupea* has a fully teleostean sensory canal system with no trace of parietal pit-lines. Within the limits of present knowledge it appears that *Mesoclupea*, which is known only from China, is derived from the group of fishes which gave rise to *Thrissops* and *Allothrissops*.

Pachythrissops is limited to Kimmeridgian (Late Jurassic) deposits of West Germany. Relationship of this genus to other chirocentrids is in doubt on account of the presence of several rather than a single row of premaxillary teeth, fulcral scales in front of the dorsal lobe of caudal fin, and a gular plate (NYBELIN, 1964, pl. 9, fig. 4). Neurocranial structure is unknown. If this fish is a chirocentrid, it is distinctly separated from the main line of chirocentrid evolution.

SAINT-SEINE was impressed by supposed differences in feeding habits of *Thrissops* and *Pachythrissops* and accordingly derived different groups of chirocentrids from these genera. He stated that *Thrissops* was a

planktivore like *Leptolepis*, but *Pachythrissops* having stout, conical teeth was a carnivore. The fishes SAINT-SEINE included in *Pachythrissops* and from which he derived information on dentition differ from true *Pachythrissops* and I believe should be excluded from this genus and the Chirocentridae (see "Systematic Descriptions"). NYBELIN (1958) demonstrated that *Thrissops* could engulf small fishes. He suggested that feeding on large prey might be seasonal and that *Thrissops* was a plankton-feeder at other times. The diet of *Pachythrissops* is unknown. Later representatives of both *Chirocentrus* and *Xiphactinus* groups are capable of engulfing large prey.

Of the four Jurassic genera, *Thrissops* has developed several characters which suggest that later chirocentrids originated from a species of *Thrissops* such as *T. subovatus*. Two Cretaceous genera, *Eubiodectes* and *Proportheus*, are closely related to Cretaceous species of *Thrissops*.

Eubiodectes, inadequately described from incomplete specimens, may be either (1) derived from some unknown Early Cretaceous species of *Thrissops*, or (2) as BASSANI (1882) suggested, a synonym of *Thrissops*. *Eubiodectes,* known only from the Cenomanian (Late Cretaceous) of Lebanon, resembles the Cretaceous *T. microdon* in shape of maxillary, enlarged dentition of irregular size, relative position of dorsal and anal fins, and number of rays in each.

The close relationship of *Proportheus* and *Thrissops* was suggested by ARAMBOURG (1954). Both genera are known from Late Cretaceous deposits in Africa. Height of the supraoccipital crest and angle of the gape of the mouth are similar in *Proportheus* and *T. vexillifer*. The premaxillary of *Proportheus* retains a ventroposterior process as in its *Thrissops* ancestors. The coronoid process of the elongate mandible is not raised sharply above the dental border. The number of vertebrae (approximately 60) is within the range of Cretaceous species of *Thrissops*. *Proportheus*, like *Thrissops*, has an anal fin of at least 30 rays and large scales with strong circuli. In other respects, *Proportheus* resembles *Chirocentrus*. Just behind the anterior end of the premaxillary a short process rises from the dorsoanterior surface of this bone. At least one enlarged anterior tooth, followed by several smaller conical teeth, occurs on the premaxillary. The slender, elongate, gently curved maxillary is not unlike that of *Chirocentrus*. Relative position of dorsal and anal fins, as well as number of rays in each fin, are similar in both genera. Among known fossil chirocentrids, *Proportheus* is the most likely ancestor of *Chirocentrus*. In view of the limited fossil evidence and incomplete anatomical knowledge of known fossils, this must be considered a tentative conclusion.

SAINT-SEINE (1949) derived *Chirocentrus* from *Ichthyodectes*. His knowledge of *Ichthyodectes* was obtained from the description of WOODWARD (1903), according to whom the supraoccipital separates parietals in *Ichthyodectes* and *Chirocentrus*. But examination of numerous *Ichthyodectes* specimens shows that parietals of this fish actually meet at the median line. SAINT-SEINE also misinterpreted fossae and grooves on the otic section of the *Ichthyodectes* neurocranium, believing that the pattern of these structures resembled those of *Chirocentrus*. WOODWARD correctly pointed out that *Chirocentrus* lacks a subtemporal fossa such as appears in *Ichthyodectes*. *Chirocentrus* is also differentiated from *Ichthyodectes* by the presence of a pre-epiotic fossa and temporal foramen. The ventral surface of the articular head of a *Chirocentrus* quadrate is transversely concave; medial and lateral sides of this head are straight. In chirocentrids of the *Xiphactinus* group this head is transversely flat, with parallel but sinuous sides.

Because definitive fossil chirocentrids are unknown between the occurrence of *Proportheus* (Late Cretaceous) and *Chirocentrus* (Recent), development of structures characteristic of the latter genus cannot be traced. These characters (absence of a subtemporal fossa and basipterygoid process, presence of an auditory fenestra, temporal foramen, pre-epiotic fossa, midsagittal frontal fontanelle, single foramen opening into trigeminofacial chamber, and position of the oculomotor nerve) appear in several living clupeoids. The presence of these characters in *Chirocentrus* may be interpreted as a parallel development under the influence of environmental pressures essentially common to early teleosts. The supposed absence of alveoli in *Chirocentrus* has been used (BERG, 1940) to divide living and fossil genera into separate families. Actually, *Chirocentrus* teeth are in shallow depressions which, considering the long geologic history of the Chirocentridae, may be interpreted as remains of alveoli. *Chirocentrus*, being smaller than those Cretaceous genera characterized by deep alveoli, would not require deep tooth emplacement. It must be emphasized, too, that chirocentrid teeth do not serve to tear prey. Therefore, teeth need not be firmly anchored in the jaws. *Chirocentrus*, distinguished from *Ichthyodectes* by a different suite of primitive and advanced characters, is closely related to the group of chirocentrids which includes Cretaceous species of *Thrissops, Eubiodectes,* and *Proportheus*.

XIPHACTINUS GROUP

Spathodactylus, the earliest member of the *Xiphactinus* group, appears only in the Neocomian (Early Cretaceous). This genus is known from a single, incomplete and inadequately described specimen. *Spathodactylus,* resembles Jurassic species of *Thrissops* in exhibiting a straight maxillary border, coronoid process not raised, mandibular dentition enlarged, vertebrae approximately 60, anal fin with more than 20 rays, and scales with circuli only. Within the limits of present knowledge it is reasonable to believe that *Spathodactylus* is derived from a Jurassic species of *Thrissops. Spathodactylus* has developed other characters which reach their fullest expression in later members of the *Xiphactinus* group. These characters include (1) body nearly 1 m. in length, (2) teeth in deep alveoli, (3) maxillary with a straight dental border and dentition of uniform size, (4) mandible with a straight alveolar border, (5) mandibular teeth enlarged relative to those of the maxillary, (6) enlarged longitudinal lateral ridge on centra, and (7) broad pectoral fin. Among known fossil chirocentrids, *Spathodactylus* is the only genus whose geologic occurrence and morphologic appearance suggest that it may be the ancestor of later members of the *Xiphactinus* group.

Prymnetes, from the Early Cretaceous(?) of Mexico, is an early derivative of the *Xiphactinus* group. Although most of the anatomy of *Prymnetes* remains unknown, assignment of this branch of chirocentrid evolution is supported by the presence of characters similar to those of several genera of this line, especially *Gillicus.* The falcate maxillary of *Prymnetes* resembles that of *Gillicus.* The lower jaw bears an elongate groove for the mandibular sensory canal like that of *Gillicus* and *Cladocyclus.* The anal fin, although incompletely preserved, was formed of less than 20 rays. The first pectoral fin ray is broad and flattened as in *Gillicus* and *Ichthyodectes.* Scales of *Prymnetes* exhibit several anterior radii as in *Gillicus.*

Except for its minute dentition, *Gillicus* exhibits all characters of the *Xiphactinus* group. The similar falcate maxillaries and ventrolaterally grooved mandibles of *Gillicus* and *Prymnetes* suggest that these fishes share a common ancestor. Sharp parasphenoid flexure, falcate maxillary, deep short mandible, and minute dentition on all jaws differentiate *Gillicus* from other genera of the *Xiphactinus* group. *Gillicus* scales resemble those of *Ichthyodectes* in the presence of posterior punctae and anterior radii, but the punctae are finer and radii discontinuous in the former. *Gillicus* appears initially in the English Albian (Early Cretaceous). In western North America *Gillicus* is definitively known from the Carlile Shale (Late Cretaceous) but, as indicated in the section on "Systematic Descriptions," a scale from the Mowry Shale (Early Cretaceous) may pertain to this genus.

The four remaining genera of the *Xiphactinus* group *(Cladocylus, Chirocentrites, Xiphactinus, Ichthyodectes)* form a closely related unit. Similarities of *Cladocyclus* and *Ichthyodectes* were noted by Woodward (1901) and Santos (1950); resemblances between *Chirocentrites* and *Xiphactinus* were cited by Woodward (1907) and similarities between *Xiphactinus* and *Ichthyodectes* have prompted a suggestion (Wilson, personal communication) that the smaller *Ichthyodectes* might be young individuals of the larger, *Xiphactinus.*

In so far as *Cladocyclus* anatomy is known, this genus has developed most of the characters of the *Xiphactinus* group. However, *Cladocyclus* includes species with a body length of nearly 1 m. *(C. gardneri),* as well as species only 15 cm. *(C. woodwardi)* long. Mandibular dentition is large and of irregular size, foreshadowing the condition in *Chirocentrites* and *Xiphactinus.* Maxillary teeth are of uniform size, as in *Spathodactylus.* The coronoid process is not enlarged. Scale radii appear on the anterior and posterior half *(C. woodwardi)* or only posterior half *(C. ferus)* of the scale, rather than being confined to the anterior half, as in *Ichthyodectes* and *Xiphactinus.* In view of these resemblances and differences, I believe that *Cladocyclus* originated before the remaining genera of the *Xiphactinus* group. *Cladocyclus* occurs only in the Late Cretaceous and is confined to South America. Saint-Seine suggested that *Platinx,* from the Eocene of Italy, was derived from the South American *Cladocyclus.* However, a small, terminal mouth, minute dentition, and elongate pectoral fin rays markedly differentiate *Platinx* from *Cladocyclus.* Inclusion of *Platinx* among the Chirocentridae remains uncertain.

The suite of primitive and advanced characters of the *Xiphactinus* group attains its ultimate development in *Chirocentrites, Xiphactinus,* and *Ichthyodectes.* Initial occurrence of these three genera in the Early Cretaceous of Europe is essentially simultaneous. *Chirocentrites* is known from Albian rocks of Italy, *Xiphactinus* and *Ichthyodectes* from Albian deposits of England. Each genus exhibits all features of the *Xiphactinus* group.

Chirocentrites retains several characters expected in the ancestor of later members of the *Xiphactinus* group. These characters include a relatively short body (approximately 75 cm. in length), abdominal centra with two and caudal centra with one longitudinal, lateral ridge, anal fin composed of 34 rays and scales lacking radii and punctae. SAINT-SEINE considered *Chirocentrites* the ancestor of *Xiphactinus*. The essentially contemporaneous appearance of these genera eliminates *Chirocentrites* from direct ancestry of *Xiphactinus*. Similar robust development of the head, angle of mouth cleft, shape of jaws, enlarged dentition of irregular size, support the opinion that *Xiphactinus* and *Chirocentrites* share a close common ancestry.

Ichthyodectes exhibits all features of the *Xiphactinus* group. The dentition is enlarged but remains of uniform size, in contrast to *Cladocyclus, Chirocentrites*, and *Xiphactinus*. Scales show anterior radii and posterior punctae, as on *Gillicus*, but radii are fewer and continuous and punctae larger and less numerous. The straight maxillary alveolar border with regularly spaced dentition of uniform size reflects the probable evolution of *Ichthyodectes* from a *Spathodactylus*-like fish.

Xiphactinus and *Ichthyodectes* are closely related. That they have many common features is evident from the descriptions of these genera. In two characters, one species, *X. gaultinus*, from the Albian of England, resembles *Ichthyodectes* and differs from later species of *Xiphactinus*. The head of the parethmoid of *X. gaultinus* is vertical, rather than directed anteriorly, as in Late Cretaceous species of *Xiphactinus*. Proportions of lateral ridges and grooves on *X. gaultinus* centra resemble those of *Ichthyodectes*. The upper jaw dentition is more uniform in size than the lower jaw dentition. In this last character *X. gaultinus* resembles both *Cladocyclus* and *Spathodactylus*. Present information suggests that either *Xiphactinus* was derived from some still unknown Early Cretaceous *Ichthyodectes* or, as is more likely, both genera share a near common ancestry.

Although specimens of *Ichthyodectes* are smaller than specimens of *Xiphactinus*, fishes referred to *Ichthyodectes* are not young individuals of *Xiphactinus*, as demonstrated by morphologic and meristic differences between these genera. *Ichthyodectes* differs from *Xiphactinus* in (1) form of palatine head of the parethmoid, which is more vertically than ventroanteriorly oriented, (2) smooth rather than rugose character of parietals at the mid-sagittal line, (3) flat rather than convex ventral surface of the parasphenoid, as well as sharper angle between the otic and orbital sections of the parasphenoid, (4) dentition of consistently uniform rather than irregular size, (5) having all pectoral fin rays divided longitudinally, in contrast to *Xiphactinus*, in which the first ray is not divided longitudinally, and (6) exhibiting abdominal scales with anterior radii rather than without them. Means and observed ranges (these figures are given in the description of each fish) of neurocranial length, jaw length, length of alveolar borders on all jaws, number of alveoli, ratio of maxillary height at palatine condyle to length of alveolar border, all differ significantly between these two genera. Upper ranges of *Ichthyodectes* jaw measurements and alveoli counts approach lower ranges of these measurements and counts in *Xiphactinus*. Although larger *Ichthyodectes* specimens have fewer alveoli, the number of alveoli in such specimens is consistently greater than those of smaller *Xiphactinus* specimens. The number of alveoli probably varies in the life of a fish, because smaller specimens of both *Ichthyodectes* and *Xiphactinus* exhibit larger numbers of alveoli than larger specimens belonging to each genus. Small individuals of *Xiphactinus* are not preserved, either because they were incompletely ossified or because such individuals occupied a different environment from the larger fishes.

RECOGNITION OF SPECIES

Eight of the 15 chirocentrid genera (*Mesoclupea Pachythrissops, Chirocentrites, Spathodactylus, Eubiodectes, Proportheus, Prymnetes, Platinx)* include only a single species. This high number of monotypic genera is perhaps accounted for by the fact that six of eight genera *(Pachythrissops, Proportheus, Spathodactylus, Prymnetes, Chirocentrites, Platinx)* are each represented by six or fewer specimens. Specimens of *Eubiodectes* are more numerous but none are complete. Recent revision (CHANG, 1963) reduced the number of species of *Mesoclupea* from two to one. This genus, according to CHANG, is known from a large number of individuals. Only *Mesoclupea, Proportheus, Eubiodectes*, and *Chirocentrites* come from more than one locality. *Thrissops, Allothrissops, Chirocentrus, Gillicus, Cladocyclus, Ichthyodectes* and *Xiphactinus* each include two or more species. *Thrissops* is the most diversified. More than a dozen species have been named but the validity of many remains to be determined. *Cladocyclus*, with five species, is the second most differentiated chirocentrid genus.

Biologically meaningful criteria for recognition of species among the three fossil genera most thoroughly examined in this study *(Xiphactinus, Ichthyodectes, Gillicus)* are difficult to determine. It has been necessary to rely on major differences in geographic occurrence and a few morphologic differences which are of doubtful significance. No distinct differences between geologically early and late specimens of these genera are recognized at present. The suggestion made in the discussion of *X. mantelli* and *X. audax*, that only one worldwide, tropical species of *Xiphactinus* may have existed is supported by widespread occurrence of certain living clupeiform species (e.g., *Albula vulpes, Elops saurus*) and several elasmobranchs. Also, genera of large living teleosts (e.g., elopids, xiphiids, istiophorids) apparently are not specifically differentiated in osteology.

The large number of species named by early students of *Ichthyodectes* and *Xiphactinus* was based on slight differences in number of premaxillary and maxillary alveoli and shape of maxillary and mandibular alveolar borders. The number of alveoli varies bilaterally, as shown in descriptions of *X. audax* and *I. ctenodon*. Shape of the alveolar border of a jaw is subject to individual variation and distortion in fossilization. Pressures on the jaws incurred in feeding on large prey may be a cause of slight variation in shape of these bones. In view of these factors, the large number of species of *Xiphactinus* and *Ichthyodectes* heretofore recognized is reduced.

ORIGIN OF CHIROCENTRIDAE

Saint-Seine (1949) derived chirocentrids from leptolepids. Gardiner (1960), in a work not principally concerned with origin of the chirocentrids, concurred in this relationship. Nybelin (1964) suggested that *Allothrissops* may be derived from either leptolepids or pholidophorids. Similarities among early teleosts and certain halecostomes (pholidophorids and leptolepids) have long been noted (Woodward, 1901). Leptolepids, for a long time better known than pholidophorids, have been considered (Rayner, 1941, 1948; Dunkle, 1940; Gregory, 1933) ancestors at least of certain clupeiform teleosts, because leptolepids and several clupeoid families show a common pattern in one or more characters. Leptolepids (primarily known from the single genus *Leptolepis*) are too specialized, especially in jaw structure, to be ancestors of all early teleosts. If primitive characters of early chirocentrids are correctly determined, leptolepids are eliminated as chirocentrid ancestors. Derivation from a pholidophorid is more likely. Anatomical knowledge of pholidophoroids (primarily the pholidophorid, *Pholidophorus* and the ichthyokentemid, *Ichthyokentema*) comes principally from Rayner (1948), Saint-Seine (1949) and Griffith & Patterson (1963). *Ichthyokentema* is more primitive than *Pholidophorus* (according to Griffith & Patterson) and the anatomy of *Ichthyokentema,* especially in regard to the neurocranium, is better known. Resemblances and differences among early chirocentrids, leptolepids, and pholidophoroids are shown in Table 2.

The principal reasons for which Saint-Seine (1949) supported derivation of chirocentrids from leptolepids include (1) exposure of supraoccipital on cranial roof in contrast to *Pholidophorus* (structure of *Ichthyokentema* unknown in 1949), and (2) coronoid process of *Thrissops* enlarged as in *Leptolepis*. But the coronoid process of the earliest and most primitive chirocentrid, *Allothrissops*, is not as steeply raised as in *Leptolepis*, and closely resembles the coronoid process of *Ichthyokentema*.

Other characters which differentiate chirocentrids from leptolepids and align them with pholidophorids are empirically determined or inferred from anatomy of later chirocentrids. These characters include (1) a well ossified snout with enlarged parethmoid, as in *Ichthyokentema*; (2) a subtemporal fossa as in (a) late Mesozoic chirocentrids, (b) elopids derived from pholidophorids (Gardiner, 1960), and (c) *Ichthyokentema*, in which a small depression probably indicative of the beginning of such a fossa appears on the lateral neurocranial wall (no evidence for this fossa seen in *Leptolepis*, despite Dunkle's (1940) statement to the contrary); (3) a deep post-temporal fossa, such as occurs in all Mesozoic chirocentrids and *Ichthyokentema*; this fossa shallow in *Leptolepis*; (4) similar position of the oculomotor nerve in *Ichthyokentema* and Cretaceous chirocentrids; (5) an essentially common development of a slender, elongate maxillary in Mesozoic chirocentrids and pholidophoroids, the deep maxillary of leptolepids being a specialization which differentiates them from chirocentrids.

In consideration of these characters I believe that chirocentrids originated from pholidophorids rather than leptolepids. Evidence offered by localities from which early chirocentrids are known suggests that these fishes originated along the northwestern margin of the Tethyian seas.

TABLE 2. *Resemblances and Differences Between Early Chirocentrids, Leptolepids and Pholidophoroids.*

STRUCTURE	LEPTOLEPID CONDITION	EARLY CHIROCENTRID CONDITION	POLIDOPHORID CONDITION
(1) supraoccipital	exposed on skull roof	exposed	exposed in *Ichthyokentema* (not *Pholidophorus*)
(2) parietals	united mid-sagittally	united mid-sagittally	united mid-sagittally
(3) parethmoid	incompletely ossified	well ossified	well ossified
(4) basisphenoid	ventral process present	ventral process present	ventral process present
(5) intercalar	small	presumed small	small
(6) subtemporal fossa	absent	presumed present	perhaps slightly developed in *Ichthyokentema*
(7) post-temporal fossa	slightly developed	moderately developed	strongly developed, especially in *Ichthyokentema*
(8) basipterygoid process	present	presumed present	present
(9) trigeminofacial chamber	present	not known	separate trigeminal and facial fenestrae
(10) oculomotor nerve	emerges through basisphenoid	probably emerges through prootic	emerges through prootic
(11) premaxillary	deep, short	shallow, elongate	shallow, elongate
(12) maxillary	deep, elongate	shallow, elongate	shallow, elongate
(13) mandible	coronoid process sharply raised	coronoid process low, not sharply raised	coronoid process low, not sharply raised
(14) dentition	minute	initially small, subsequently enlarged	larger than in leptolepids
(15) centra	slightly constricted; no longitudinal ridge	constricted; slight longitudinal, lateral ridge	unconstricted; no lateral ridge

The Saurocephalidae (=Saurodontidae) resemble Cretaceous chirocentrids of the *Xiphactinus* group, especially *Xiphactinus* and *Ichthyodectes*. Saurocephalid neurocrania are longer and lower than those of *Xiphactinus* or *Ichthyodectes* but the morphology of dorsal and lateral surfaces is similar. The proportions of lateral ridges and grooves on the centra resemble those of *Gillicus*. Saurocephalids differ from chirocentrids in the presence of an edentulous predentary, and a series of foramina on the medial margins of each jaw. These foramina are equivalent in number to the alveoli on the dental margins of each jaw. The lower jaw is longer and proportionally shallower at the symphysis and coronoid process than in chirocentrids. Teeth are laterally compressed rather than conical. Saurocephalids first appeared in the Late Cretaceous but must have had a long history before this time. The characteristic predentary and medial jaw foramina remove any chirocentrid from consideration as an ancestor of the saurocephalids. However, it cannot be doubted that among known fossil teleosts, saurocephalids are most closely related to chirocentrids.

MORPHOLOGIC COMPARISON OF EARLY CLUPEIFORMES AND THEIR ANCESTORS

A brief discussion of morphological similarities and differences among geologically early clupeiforms and their ancestors is necessary in order to demonstrate the evolutionary divergence of these fishes and identify the ancestors of each early clupeiform family. No review emphasizing paleontologic evidence and covering more than one or two families previously has appeared. In this section, the anatomy of seven teleostean and three halecostome families is discussed. The teleostean families, including the first fishes to reach the teleostean structural level, are characterized by a mosaic of primitive teleostean features (some of which simply have been retained from their halecostome ancestors) and specialized structures representing adaptive modifications of the feeding and locomotor mechanisms of each family. Of the seven families, more information is available on the anatomy of chirocentrids, elopids, and clupeids than of the four other families. Therefore, the structure of the three mentioned families is emphasized in this comparative discussion. Knowledge of clupeid anatomy and to a lesser degree elopid anatomy is derived from living fishes. The seven teleostean families are compared with leptolepids, pholidophorids, and ichthyokentemids in order to demonstrate resemblances between certain teleosteans and halecostomes.

Geologically early clupeiforms including anatomically better known fossil and living genera are listed below.

Clupeiform Families

Order Clupeiformes
- Clupavidae (U. Jur.-Cret.), *Clupavus.* [According to ARAMBOURG (1954) this family is closely related to the Dussumieridae (Oligo.-Recent) including *Dussumieria.*]
- Clupeidae (?L. Cret., U.Cret.-Rec.), *?Crossognathus, Clupea*
- Chanidae (U. Cret.-Rec.), *Parachanos, Chanos*
- Chirocentridae (M. Jur.-Rec.), *Allothrissops, Thrissops, Xiphactinus, Gillicus, Chirocentrus*
- Saurocephalidae (U. Cret.), *Saurocephalus, Saurodon*
- Elopidae (?Jur., Cret.-Rec.), *Notelops, Elops, Tarpon*
- Pachyrhizodidae (U. Cret.), *Pachyrhizodus, Thrissopater*

Teleostean ancestors including the anatomically better known halecostomes are the following.

Superorder Halecostomi
- Order Pholidophoriformes
  - Pholidophoridae (M. Trias.-U. Jur.), *Pholidophorus.*
  - Ichthyokentemidae (M. Jur.), *Ichthyokentema.* [This genus is not directly ancestral to any teleost but many structures expected in still unknown or incompletely described early teleosts and late halecostomes are exhibited by *I. purbeckensis* (DAVIES).]
- Order Leptolepiformes
  - Leptolepidae (U. Trias.-L. Cret.), *Leptolepis, Anaethalion.*

Except for chirocentrids, information on structure of these halecostomes and early clupeiforms comes from RIDEWOOD (1904a, 1904b), ARAMBOURG & SCHNEEGANS (1936), RAYNER (1937, 1948), DUNKLE (1940), SAINT-SEINE (1949), ARAMBOURG (1954) and GRIFFITH & PATTERSON (1963).

Body shape generally has little or no significance in tracing relationships and origins of teleosts. However, major deviations from the short, fusiform body characteristic of most early teleosts and their halecostome ancestors must be noted because such differences imply changes in locomotor and feeding adaptations. The elongate, laterally compressed chirocentrids have diverged more than other early clupeiforms from the typical herring-like body shape.

CRANIAL CHARACTERS

Characteristic and phylogenetically significant differences are observed in cranial structure. In pholidophorids, ichthyokentemids, leptolepids, elopids, and chanids the neurocranial roof is flat, in clupeids slightly ridged, and in chirocentrids and saurocephalids high ridges are pronounced features of the neurocranium. These ridges comprise a central element formed by the supraoccipital and a pair of dorsolateral ridges formed of frontal, parietal, and epiotic. Dorsolateral ridges are present in clupeids. Dorsolateral and central ridges appear in chirocentrids and saurocephalids. Such ridges and the grooves between them increase surface area for attachment of trunk musculature. In pholidophorids, ichthyokentemids, and elopids, epaxial muscles extend anteriorly beneath the dorsal surface of the neurocranium through post-temporal fossae. Epaxial muscles of holosteans are restricted to the posterior neurocranial surface. Insertion of epaxial muscles farther forward, either on top of or below the dorsal neurocranial surface, increases their leverage for raising the neurocranium in the manner described by TCHERNAVIN (1953). The advance of trunk musculature over the neurocranium is characteristic of early teleost evolution.

A prominent sphenotic process extends laterally from the neurocranial roof in elopids, chirocentrids, and saurocephalids but is barely developed in pholidophorids, leptolepids, and early chanids. With increased freedom of palatal movement in teleosts, the sphenotic process becomes functionally important, because muscles moving the hyomandibular arise from this process.

Frontals are narrow, elongate bones in all early clupeiform fishes. In *Chanos* these bones have become secondarily short and broad. This condition represents a specialization because the Cretaceous *Parachanos* has narrow frontals. An elongate fontanelle appears between each frontal just behind the frontoethmoid suture in clupeids and *Chirocentrus*, but not in elopids, fossil chirocentrids, or halecostomes.

The vomeroethmoid unit (including parethmoid) provides support for palatine and upper jaws. In chirocentrids this unit is fully ossified and multifaceted, providing a firm interlocking attachment for the anterior end of the hyopalatine arch and bracing for upper jaws. The chirocentrid vomeroethmoid block is thus able to absorb thrusts imparted by large prey which these fishes engulf. In *Notelops, Elops*, and *Clupea*, fishes not swallowing large prey, the vomeroethmoid block contains extensive portions of cartilage. The snout of *Leptolepis* is incompletely ossified, whereas that of *Ichthyokentema* is firmly ossified. The parethmoid of *Ichthyokentema*, and to a lesser degree that of *Pholidophorus*, resembles the parethmoid of chirocentrids. A rostral element is present in halecostomes but not in clupeiforms.

Evolutionary significance of different topographic relationships of supraoccipital, parietals, and frontals has been discussed by several authors (RIDEWOOD, 1904a; WOODWARD, 1901). The paired parietals may be joined at the mid-sagittal line of the neurocranium or separated from each other by union of supraoccipital and frontals. In clupeids, chanids, and dussumierids, parietals are separated by supraoccipital-frontal contact.

Parietals are joined mid-sagittally in clupavids. The relationship of parietals, frontals, and supraoccipital may vary within members of one family. Some chirocentrids *(Allothrissops, Xiphactinus, Gillicus)* exhibit parietal contact at the mid-sagittal line, but supraoccipital-frontal contact characterizes *Thrissops vexillifer* and *Chirocentrus*. Parietal contact is characteristic of geologically early members of this family. Elopids show an elongate, mid-sagittal parietal connection. In pachyrhizodids parietals are reduced and the supraoccipital joins the frontals. Because parietals are united in pholidophorids, ichthyokentemids, and leptolepids, this condition must be recognized as primitive in early teleosts. Junction of supraoccipital and frontal represents an advanced condition. Supraoccipital-frontal juncture may occur beneath conjoined parietals (Woodward, 1901). Relationships of these bones are in a state of flux associated with remolding of the neurocranium which is occurring in early teleosts.

The shape of the parasphenoid and processes arising from this bone differ among early clupeiforms and halecostome ancestors. The parasphenoid may lie parallel to the longitudinal body axis or the orbital section of this bone may be bent sharply upward relative to the postorbital section. The parasphenoid is strongly angled in chanids, straight or slightly angled in clupeids, and straight in dussumierids. In primitive elopids *(Elops, Notelops)* the parasphenoid is straight but in the more specialized *Tarpon* this bone is bent. Among chirocentrids this bone lies parallel to the body axis or is bent. According to Kirchhoff (1958) the parasphenoid is more strongly bent in fishes with enlarged eyes. The eye of *Gillicus* is proportionally larger than that of *Xiphactinus* and the parasphenoid angle decidedly stronger. The strong arch of the parasphenoid also may be related to development of an enlarged orobranchial chamber. Tchernavin emphasized upward movement of the vomeroethmoid block as part of the process involved in raising the head in order to produce a wide gape of the mouth. The sharp angle of the *Gillicus* parasphenoid is such that the vomeroethmoid block would rise higher than that of *Xiphactinus* when the head of each fish is raised an equal degree. The smaller *Gillicus* would have a relatively deeper orobranchial chamber than the larger *Xiphactinus*.

A lateral projection of the parasphenoid, the basipterygoid process, appears in *Xiphactinus, Ichthyodectes, Gillicus, Leptolepis, Pholidophorus,* and *Ichthyokentema*. Such a process must have existed in *Allothrissops* and *Thrissops* (see section on "Evolution of Chirocentrid Fishes"). Immediate ancestors of *Chirocentrus* perhaps possessed a basipterygoid process, because the mesopterygoid and metapterygoid retain a notch where this process would be received. The basipterygoid process, essentially a holostean feature, is not developed in other clupeiform families under discussion. This process anchors the palate to the neurocranium, restricting anteroposterior palatal movement. Fossil chirocentrids have retained this process in order to brace and stabilize the enlarged hyopalatine arch which is subjected to strong forces in a posterolateral direction by the large prey which these fishes swallowed. The ascending process of the parasphenoid is a slender vertical bar in *Leptolepis*. This process is shorter and more anteroposteriorly elongate in *Ichthyokentema, Pholidophorus*, and *Notelops*. In chirocentrids the ascending process is elongate and forms almost half of the myodome wall in some fossil genera.

The basisphenoid has a short, mid-sagittal vertical process in *Clupea* but this process is absent in other clupeids and *Chirocentrus*. A stout vertical process reaching the parasphenoid appears in halecostomes, elopids, and fossil chirocentrids. The basisphenoid is absent in chanids.

The basioccipital is large in Cretaceous chirocentrids, chanids, pholidophorids, ichthyokentemids, and leptolepids, whereas in *Chirocentrus* and clupeids this bone is reduced, concomitantly with expansion of the exoccipital and prootic bones. The intercalar is enlarged in *Tarpon* but not in *Elops* or *Notelops*. In *Xiphactinus, Ichthyodectes,* and *Gillicus* the intercalar is relatively larger than in other clupeiform fishes. This bone provides additional surface for articulation of the hyomandibular and strengthens the posterolateral corner of the neurocranium. In *Chirocentrus* and other early clupeiforms the intercalar remains small and does not articulate with the hyomandibular.

DEPRESSIONS AND OPENINGS OF NEUROCRANIUM

Fossae, foramina, and fenestrae on postorbital and lateral walls of the neurocranium have been studied in *Pholidophorus, Ichthyokentema, Leptolepis, Xiphactinus, Chirocentrus*, and several living clupeids (Tracy, 1920). The arrangement of these openings and pits is similar among families represented by these genera. Pathways of blood vessels and nerves have been rather conservative in the evolution of early teleosteans. Nev-

ertheless, significant differences are observed among these fishes.

One or more fossae may appear on the neurocranium of clupeiforms and halecostomes. These include post-temporal, subtemporal, subepiotic and preepiotic fossae. An anteroposteriorly elongate, deep post-temporal fossa is excavated beneath the dorsal surface of the neurocranium in pholidophorids and ichthyokentemids. A similar but less elongate fossa is developed in leptolepids. A post-temporal fossa is retained in elopids, pachyrhizodids, Mesozoic chirocentrids, and *Chanos*. Erosion of the parietal and pterotic bones which roof the post-temporal fossa produces a post-temporal groove, rather than a fossa, in clupeids and *Chirocentrus*.

A subtemporal fossa below the articular facet for the hyomandibular is a feature of elopids, albulids, and several chirocentrids. This fossa appears in other teleosts including *Osteoglossum* and cyprinids. Such a fossa is developed in pholidophorids but not in leptolepids. Clupeids and *Chirocentrus* lack a subtemporal fossa. The subtemporal fossa provides an extensive area for the origin of levator muscles of the branchial arches. Presence or absence of this fossa is functionally, as well as phylogenetically, significant. This fossa occurs in teleosts derived from pholidophorids but not in those derived from leptolepids. This fossa is not present in all members of a family, being confined generally to geologically earlier or more primitive members of a particular family.

A preepiotic fossa appears in *Clupea* and *Chirocentrus* but not in *Chanos* or fossil chirocentrids. It is not present in pholidophorids, leptolepids, or elopids. A subepiotic fossa has been described in clupeids and chirocentrids but not in elopids, pholidophorids, or leptolepids. This shallow depression provides additional surface for attachment of epaxial muscles and is not developed where an elongate post-temporal fossa is present.

A temporal foramen opening into the endocranial cavity and containing a diverticulum of the sensory canal system appears in clupeids and *Chirocentrus* but not in fossil chirocentrids, *Chanos*, and elopids. Whether this opening is present in *Parachanos* or Cretaceous clupeids is not known. The sensory canal system has, no doubt, changed in the course of teleostean history and apparently several not directly related living teleosts have developed similar sensory canal structures. Thus, *Chirocentrus* and clupeids resemble each other in development of a temporal foramen.

The auditory fenestra, a neurocranial opening lateral to the saccular recess, is surrounded by prootic, exoccipital, and basioccipital bones. This fenestra appears in *Chirocentrus* and clupeids. Dissection of a *Tarpon atlanticus* shows that an auditory fenestra also occurs in this genus, but such a fenestra cannot be positively identified in fossil chirocentrids. The concave lateral wall of the basioccipital in fossil chirocentrids was probably covered by an anterior extension of the swim-bladder which ended against the thin lateral wall of the saccular recess. Prootic and pterotic osseous capsules for diverticula of the swim-bladder are present in clupeids and *Chirocentrus* but not in elopids or fossil chirocentrids.

Cranial nerves I and II emerge through the orbitosphenoid and optic foramen, respectively, in all families under consideration. The oculomotor nerve (III) leaves the neurocranium through the lateral plate of the basisphenoid in *Leptolepis* and *Chirocentrus*. This nerve enters the orbit through the prootic medial to the trigeminofacial chamber in *Xiphactinus, Ichthyodectes*, and elopids. In clupeids the path of the third nerve lies between the basisphenoid and prootic. In *Ichthyokentema* the oculomotor nerve emerges from the endocranium through the optic foramen. The position of this nerve in *Pholidophorus* is uncertain but it probably emerged through the optic foramen.

The trochlear nerve (IV) enters the orbit through the optic foramen in halecostomes and such is probably the case in early teleosts. This nerve emerges through the pterosphenoid in *Clupea*. In *Chirocentrus* the trochlear nerve leaves the neurocranium through the pterosphenoid just dorsal to the trigeminofacial foramen. The sixth nerve in all fishes under discussion enters the posterior myodome canal via a foramen in the medial wing of the prootic.

The trigeminofacial chamber is surrounded by pterosphenoid and prootic in clupeids and *Chirocentrus*, and by prootic in leptolepids, elopids, and fossil chirocentrids. *Pholidophorus* and *Ichthyokentema* retain separate trigeminal and facial foramina. Four openings from the endocranial cavity lead into the trigeminofacial chamber in *Leptolepis*, two in *Xiphactinus* and *Notelops* but only a single opening appears in *Chirocentrus*, clupeids, and living elopids. Components of the fifth and seventh nerves, lateral head vein, and orbitonasal artery emerge through these foramina. A trend toward reduced ossification of the post-orbital neurocranial wall characterizes the evolutionary history of clupeiforms.

In all clupeiform families the hyomandibular branch of the seventh nerve emerges through a foramen near the dorsoanterior corner of the lateral neurocranial wall. A second foramen lies ventral to the opening for the hyomandibular branch of the seventh nerve. This foramen carries a posterior palatine branch of the seventh nerve and perhaps also the orbitonasal artery. In *Notelops* and some individuals of *Xiphactinus* this artery may enter the prootic through a third, smaller, ventrolateral foramen.

The otic branch of the seventh nerve emerges through the trigeminofacial chamber, extends dorsally and enters the sphenotic through a foramen in the orbital face of this bone in leptolepids and chirocentrids. The otic branch remains entirely within the neurocranial wall in clupeids. In *Notelops* the otic branch emerges from the lateral surface of the neurocranial wall along with the hyomandibular branch of the seventh nerve. A foramen for the otic branch of the seventh nerve appears on the orbital face of the sphenotic in *Ichthyokentema* and *Pholidophorus*.

Cranial nerves 9 and 10 emerge from the posterolateral corner of the neurocranium in all fishes under discussion. The supratemporal branch of the 9th nerve may emerge laterally through the prootic *(Ichthyokentema)* or posteriorly through the exoccipital *(Xiphactinus)*.

The supraorbital sensory canal is not connected to the lateral line canal in halecostomes. *Clupavus* retains a branch of the supraorbital sensory canal which reaches the posterior edge of the frontal as in halecostomes but this fish also has developed a supraorbital-lateral line connection as in all teleosts (Arambourg, 1954).

JAWS, TEETH, AND OTHER SKULL CHARACTERS

Structures of the upper and lower jaws and dentition characterize each family. Differences in jaw and tooth development reflect adaptive modifications in the feeding mechanism of each family. In all genera except *Chanos*, premaxillary and maxillary form the upper border of the mouth. The premaxillary alone borders the mouth in *Chanos*. The premaxillary of fossil chirocentrids, saurocephalids, and dussumierids is firmly united to a dorsoventrally expanded anteromedial section of the maxillary. This relationship between premaxillary and maxillary produces a stable upper jaw and strengthens the lateral margin of the mouth. In chirocentrids the upper jaw must withstand lateral thrusts produced by large prey entering the orobranchial chamber. Connection of premaxillary and maxillary in clupeids, clupavids, and elopids is largely ligamentous. The premaxillary of *Pholidophorus* lies in a depression on the anterolateral surface of the maxillary. This condition is expected in an ancestor of chirocentrids. The *Leptolepis* premaxillary lies below a dorsoanterior projection of the maxillary and must have been connected primarily by ligaments to the maxillary.

The premaxillary is connected to the ethmoid by ligaments only in *Dussumieria, Xiphactinus,* and *Ichthyodectes*. In these fishes the maxillary alone articulates with the ethmoid. Both premaxillary and maxillary meet the ethmoid in clupeids, clupavids, and elopids. The premaxillaries of *Dussumieria, Xiphactinus, Gillicus*, and several other chirocentrids lack a ventroposterior projection. This projection must have been lost in the evolution of these fishes because such a process is present in Jurassic teleosts and their halecostome ancestors.

The maxillary is an elongate slender bone in pholidophorids, chirocentrids, and elopids. The *Leptolepis* maxillary has become short and deep, whereas that of *Anaethalion* retains the slender elongate shape of its pholidophorid ancestors. The maxillary of clupavids and most clupeids resembles that of *Leptolepis*. Except for clupavids, chanids, and dussumierids, the posterior end of the maxillary lies below or behind the middle of the orbit. The maxillaries of clupavids, chanids, and dussumierids have become shorter in correlation with anterior movement of the quadrate-mandibular joint. In addition to the connection between maxillary and ethmoid, the maxillary also abuts on the palatine dorsally. In elopids, clupeids, and *Chirocentrus*, palatine and maxillary articulate by a ball-and-socket joint. A flat surface forms the junction between these bones in *Xiphactinus, Ichthyodectes,* and probably *Thrissops*. Little if any rotation of maxillary on the palatine was possible in these fishes. Thus, in still another feature these chirocentrids are specialized to strengthen the feeding apparatus. There are two supramaxillaries in all early clupeiforms. *Ichthyokentema* has a single supramaxillary but *Pholidophorus* and *Leptolepis* each show two.

Resemblances in mandibular shape provide significant evidence of relationships among early teleosts and their ancestors. Elopids, pachyrhizodids, chirocentrids and saurocephalids have elongate, shallow mandibles without an elongate steeply raised coronoid process.

Pholidophorus exhibits an elongate mandible. The short coronoid process of this fish does not rise sharply from the dental border. The mandible of *Ichthyokentema* is relatively shorter than that of *Pholidophorus* and the elongate coronoid process is formed by dentary and angular. The *Leptolepis* mandible is short and deep, with a steeply raised, elongate coronoid process also comprising dentary and angular. The mandible of *Anaethalion* is relatively shallower and without the steeply raised coronoid process of *Leptolepis*. The mandible of most clupeids resembles that of *Leptolepis*. In genera with a deep mandible the dental margin is short and the gape of the mouth is limited (GÜNTHER, 1953) by the coronoid process. Dermangular and autangular are fused in clupeids and *Chirocentrus*. These bones remain separate in *Xiphactinus, Ichthyodectes* and elopids. A separate retroarticular appears in chirocentrids and *Clupea* but not in elopids.

Minute or enlarged, generally conical teeth line the jaw margins of all fishes under consideration except chanids and clupavids(?). Dentition may be developed in a single row of minute teeth as in clupeids and dussumierids, a single row of large teeth as in chirocentrids and saurocephalids, or multiple rows of minute teeth as in elopids. *Ichthyokentema* has a single row of small teeth on the upper jaw and a patch of teeth on coronoid and dentary. *Pholidophorus* exhibits several rows of small teeth on upper and lower jaws. Teeth are inserted in sockets in most chirocentrids and saurocephalids. In *Pachyrhizodus* teeth are fused at their expanded bases to the dental margin and medial wall of maxillary and mandible. Premaxillary teeth of *Pachyrhizodus* are inserted in small depressions (?alveoli) along the dental border. Clupeid teeth are loosely attached to the jaws by connective tissue. Saurocephalids exhibit a series of foramina or deep grooves on the medial side of each jaw below each alveolus. Tooth buds of replacement teeth enter each socket through these foramina. The presence of enlarged teeth in such fishes as the chirocentrids does not mean that these fishes slash or break up their prey prior to swallowing it. The preservation of complete fish within the abdominal cavities of specimens of *Thrissops, Xiphactinus,* and *Chirocentrus* demonstrates rather that these fishes engulfed their prey intact. The enlarged teeth serve to hold and direct the prey while it is being swallowed.

A gular is present in halecostomes and elopids. This bone is absent from chirocentrids, clupeids, chanids and clupavids.

Information on hyopalatine structure of fossil Clupeiformes is inadequate. Functionally and probably phylogenetically significant differences in hyopalatine structure involve those parts of this unit which articulate with neurocranium and jaws, namely hyomandibular, palatine and quadrate. The hyomandibular of halecostomes has a dorsally rounded neurocranial head. The clupeid hyomandibular exhibits a flat or divided neurocranial head. In *Tarpon* the neurocranial head is flat whereas in *Elops* it is divided. The hyomandibular is vertically oriented in halecostomes and to a greater or lesser degree anteriorly directed in early clupeiforms. The palatine head is small in elopids, moderately enlarged in clupeids and dussumierids, and massive in chirocentrids. In fishes with an enlarged palatine head this element is firmly interlocked with the vomeroethmoid block.

The sclerotic ring of *Allothrissops* is a single bone. In other chirocentrids this ring is composed of two bones. The *Notelops* scleral ring is formed of five bones, whereas that of *Leptolepis* comprises two bones, and the scleral ring of *Ichthyokentema* one bone. Suborbital and antorbital bones are present only in *Pholidophorus, Ichthyokentema* and one species of *Leptolepis (L. coryphaenoides)*.

The posteroventral corner of the preoperculum in *Thrissops* forms a right angle. A similar but less sharp angle characterizes this bone in other chirocentrids. In contrast, the posteroventral preopercular margin is rounded in *Pholidophorus, Ichthyokentema,* clupeids, dussumierids, and elopids. The shape of operculum, suboperculum, and interoperculum tends to differ among genera of one family.

Differences in gill rakers are related to feeding habits. Unfortunately these structures are poorly preserved and undescribed in most fossil teleosts. Gill rakers of clupeids are long, slender, and smooth, In elopids these structures are slender and coarse. *Chirocentrus, Xiphactinus,* and *Gillicus* possess spikelike gill rakers with characteristic tooth plates attached to each raker. The opinion that these genera are closely related is supported by occurrence of such similar rakers in these fishes.

POSTCRANIAL CHARACTERS

The number and structure of vertebrae varies among early clupeiforms. Elopids include species with 60-80 vertebrae. Vertebral counts of clupeid genera range from 40-60. Among chirocentrids some species of *Cladocyclus* have 40 centra, whereas *Xiphactinus* averages 85. Most chirocentrids exhibit 55-65 vertebrae.

Body length of Clupeiformes is related to number of vertebrae. The larger chirocentrids have higher vertebral counts. Centra of most chirocentrids exhibit a pair of deep, elongate lateral groovees above and below a stout longitudinal ridge. *Chirocentrus* and *Pachythrissops* show several slender longitudinal ridges. Dorsal and ventral depressions are present on chirocentrid centra for neural and hemal arches. The arches are not fused with the centra as in clupeids. Saurocephalid centra resemble those of chirocentrids. Clupeid centra show one or more narrow longitudinal lateral ridges. Centra of elopids and pachyrhizodids may be laterally smooth or show a fine network of slender ridges. Neural and hemal arches are not fused to centra in elopids and pachyrhizodids. *Pholidophorus* vertebrae formed of separate pleuro- and hypocentra exhibit a large notochordal canal. *Ichthyokentema* centra are thin cylinders of bone with a large notochordal canal. Leptolepid centra are slightly constricted.

Ichthyokentema and probably *Pholidophorus* lack intermuscular bones. Dorsal intermuscular bones (epineurals, epipleurals) are present in *Leptolepis*. Chirocentrids and probably elopids have epipleural and epineural intermuscular bones, clupeids exhibit epipleural, epineural and hypopleural intermuscular bones.

The first pleural rib arises from the second centrum in *Xiphactinus* and from the fourth centrum in *Chirocentrus*. Pleural ribs of living clupeids begin on the first centrum. Anterior pleural ribs are shorter than those of mid-body. Also, anterior abdominal centra are shorter than mid-body centra. These changes in position and size of pleural ribs and abdominal centra are correlated with changes in the posterodorsal portion of the neurocranium. Together these modifications enable teleosts to raise their heads sharply in the manner described by Tchernavin (1953). Increased flexibility of the anterior part of the body can be coupled with steep depression of the lower jaw to produce a great dorsoventral expansion of the orobranchial chamber. Through such an expanded opening large prey can be engulfed or copious amounts of plankton can be drawn.

The caudal skeleton of living clupeiforms has been described by Hollister (1936) and Gosline (1960). Arambourg & Schneegans (1936) showed that the caudal skeleton of the Cretaceous *Parachanos* and Recent *Chanos* are similar. As far as can be determined from fossil specimens, the caudal skeletons of the Cretaceous *Xiphactinus* and Recent *Chirocentrus* are similar. The structure of the caudal skeleton is conservative in teleostean history. The caudal skeleton of *Ichthyokentema* and *Pholidophorus* is unknown. *Leptolepis* hypurals are expanded in some species (*L. coryphaenoides*) but not in others (*L. sprattiformis*).

Structure of the pectoral girdle is inadequately known in fossil clupeiforms. The scale bone is absent in *Allothrissops salmoneus* but this bone is present in *Thrissops vexillifer* and *Chirocentrus*. Elopids retain a broad thick scale bone, as in leptolepids and pholidophorids. In clupeids this bone is small, as in *Chirocentrus*. Dussumierids and chanids retain a large scale bone. This bone, therefore, is not absent from all teleosts as Saint-Seine (1949) stated. In early clupeiforms, in contrast to halecostomes, the post-temporal is oriented vertically and except in elopids does not form a bony roof above the body.

The mesocoracoid of *Xiphactinus, Ichthyodectes, Elops, Tarpon* and some clupeids (Starks, 1930) is united ventrally with the scapula. In *Chirocentrus* the ventral end of the mesocoracoid is sutured to the coracoid only. Pectoral actinosts of chirocentrids include a characteristic "T-shaped" proximal first and second actinost. These are articulated to distal actinosts. This articulated arrangement is more primitive than the condition in *Elops* (Starks, 1930).

Differences in position on the body of unpaired fins characterize elopids, clupeids, and chirocentrids. The dorsal and anal fins of chirocentrids are remote from the snout. In clupeids and elopids the dorsal fin arises midway along the dorsal body margin and in front of the anal fin. Traces of dorsal fin fulcral scales are retained in *Megalops*. Other teleosts lack these fulcra which occur in all halecostomes.

Scales of chirocentrids are thin, usually deciduous, and dorsoventrally elongate. Elopid scales are thick and deeply imbricated. Cells are present in scales of pholidophorids and elopids but not those of leptolepids (Gardiner, 1960). Size and ornamentation of scales differ from one group of fishes to another depending upon the part of the body from which a scale is obtained. Nevertheless, similarly located scales on different fishes of one family tend to show comparable structure on anterior and posterior halves. Scales of most Cretaceous chirocentrids exhibit anterior radii and posterior punctae. Clupeid scales have a characteristic distribution of transverse radii which may extend across the entire scale. *Elops* and *Tarpon* scales are marked by anterior radii converging toward a central

nucleus. Pholidophorid and leptolepid scales retain a coating of ganoine. This layer is absent from all early clupeiform scales except those of earliest clupavids.

In summary, structural modifications involved in origin of clupeiform fishes are observed primarily in the neurocranium (formation of ridges, fossae), jaws (mandible with or without a coronoid process, maxillary firmly or weakly joined to premaxillary), vertebrae (fusion or nonfusion of neural and hemal arches to centra) and fins (position of dorsal fin).

ORIGINS AND RELATIONSHIPS OF EARLY CLUPEIFORMES

Actinopterygian fishes are divided into three structural levels of organization—chondrostean, holostean, and teleostean. Teleosts are derived from an advanced group of holostean families that are often separated as the superorder Halecostomi. Among these early Mesozoic fishes, as already mentioned, the ancestors of teleosts were included in two families, Pholidophoridae and Leptolepidae.

The primitive teleosts contained in the order Clupeiformes are now thought to have been evolved in two lines, as indicated previously, one from pholidophorids, the other from leptolepids. In clupeiform fishes the pelvic fins are abdominal in position and have more than five rays, there are no spiny rays in the fins, the maxillary forms a functional part of the margin of the upper jaw, the scales if present are usually cycloid, the air bladder, if present, has a duct to the esophagus, the orbitosphenoid and mesocoracoid are generally present, the branched rays of the caudal fin are usually 17, and the lateral line if present is not low on the sides.

Previous studies of teleostean origins with an emphasis on paleontologic history include papers by Arambourg (1954), Arambourg & Schneegans (1936), Dunkle (1940), Rayner (1937, 1941, 1948), Saint-Seine (1949) and Woodward (1942). Relationships among living clupeiforms were considered by Gosline (1960).

Woodward (1942) suggested that some holosteans other than pholidophorids or leptolepids may have been ancestral to certain teleosts. He reached this conclusion by tracing resemblances in isolated characters generally representing specializations of particular groups of holosteans and teleosteans. Gosline (1960) concluded from a study of caudal skeleton structure in living clupeiforms that elopids formed the base of the teleostean lineage and gave rise to clupeids, chirocentrids, and chanids. Elopids are certainly the most primitive of living teleosteans. But morphology of other parts of the body than caudal skeleton, as well as the time of geologic occurrence of these fishes, indicate that elopids are not ancestors of clupeids or chirocentrids. An accurate reconstruction of teleostean origins and relationships can be made only when several structures are examined and the time of geologic appearance considered.

Teleosts first appeared in the Middle Jurassic but were not abundant and taxonomically diversified until the Late Cretaceous. The Tertiary record of most clupeiforms is scanty. Tertiary teleosts commonly are morphologically similar to existing genera. Despite the long span of geologic time, structures characteristic of living clupeiform fishes were established well before the close of the Cretaceous. The first chirocentrid is known from the Middle Jurassic (Bathonian). Definitive elopids appeared in the Early Cretaceous. However, Nybelin (1961) suggested that fishes referable to this family may have been in existence by the late Jurassic (Kimmeridgian). He cited still undescribed West German fossils which exhibit a strong resemblance to *Elops*. Clupeids are certainly recognized in the Late Cretaceous and perhaps even in the Early Cretaceous (Neocomian), if *Crossognathus* is a clupeid. Clupavids are first recorded from the Late Jurassic (Purbeckian). Pholiodophorids first appeared in the Middle Triassic (Gardiner, 1960) and survived until Late Jurassic. The earliest leptolepid comes from the Late Triassic (Saint-Seine, 1949) and the latest is known from the Early Cretaceous. The fossil record of clupeiforms prior to the Late Cretaceous is limited to less than a dozen genera. Many pre-Late Cretaceous teleosts have not been studied since the 19th century. Structural diversity of these teleosts, as well as their halecostome ancestors, is greater than now generally known (Nybelin, 1961, 1964). It is probable that more clupeiform families than now recognized were in existence prior to the Late Cretaceous. Differences between the halecostomes *Leptolepis* and *Anaethalion* in form of the neurocranial roof and mandible indicate a greater diversity among the Leptolepidae than is presently recognized taxonomically.

Derivation of chirocentrids from pholidophorids was demonstrated in the section on "Evolution of Chirocentrid Fishes." The origin of elopids from pholidophorids has been suggested by several authors

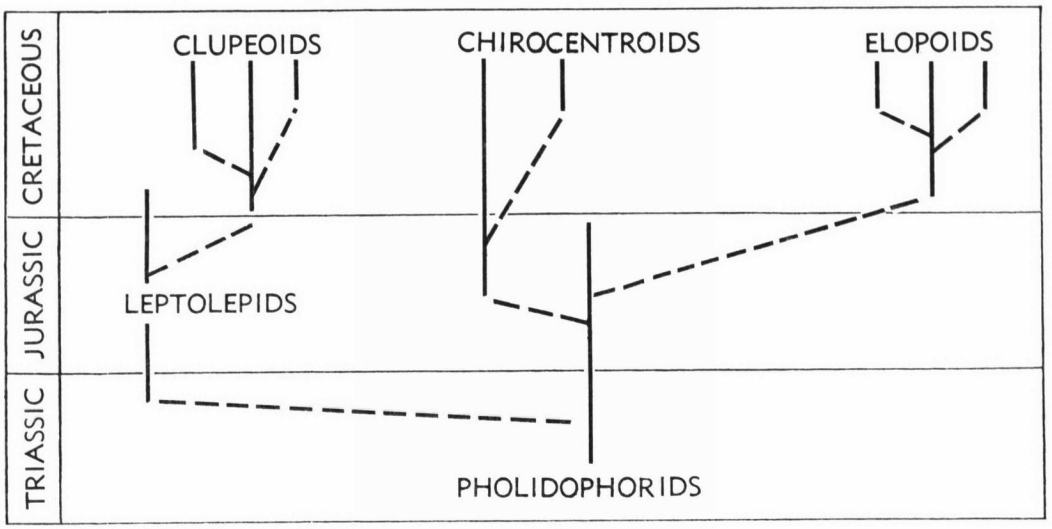


FIGURE 4. Origin and relationships of early clupeiform fishes.

(GARDINER, 1960; SCHAEFFER & ROSEN, 1961). Fishes of these two families share a common pattern of neurocranial and jaw structure. Neurocrania of pholidophorids and elopids have a flat roof, enlarged parietals united mid-sagittally, no supraoccipital or epiotic crest, an elongate post-temporal fossa and a subtemporal fossa. Pholidophorids and elopids show a firmly united premaxillary and maxillary, straight maxillary dental border, no coronoid process or only a short process barely raised above the dental border, minute teeth, and a gular plate.

The derivation of clupeids from leptolepids is generally accepted. Similarities in shape of the upper and lower jaws and to a lesser degree similarities in neurocranial structure adequately demonstrate this relationship. Clupavids known only from the Mesozoic are sufficiently similar to leptolepids and clupeids (ARAMBOURG, 1954) as to leave no doubt that both clupavids and clupeids are leptolepid derivatives.

Elopids, along with the closely related albulids and pachyrhizodids, have been united in the suborder Elopoidea (ARAMBOURG & BERTIN, 1958; GOSLINE, 1960) in recognition of the distinct suite of primitive teleostean structures retained by these fishes. Likewise clupeids, clupavids, and dussumierids have been grouped in the suborder Clupeoidea in recognition of the specializations which characterize this group of early Clupeiformes. Chirocentrids have been assigned to the Clupeoidea or given separate subordinal rank (BERG, 1940). As a group, chirocentrids are sufficiently different from other early clupeiforms in shape of body, structure of neurocranium, form of jaws, size and placement of teeth and position of medial fins to warrant their distinction as the suborder Chirocentroidea.

Although Mesozoic chirocentrids retain a number of characters in common with pholidophorids, the Recent genus *Chirocentrus* resembles clupeids in (1) development of supraoccipital-frontal contact and reduced parietals, (2) presence of a post-temporal groove, (3) lack of a basipterygoid process, (4) lack of a subtemporal fossa, (5) presence of a preepiotic fossa, (6) presence of a temporal foramen, (7) presence of an auditory fenestra, (8) presence of prootic and pterotic bullae for diverticulae of the swim bladder, and (9) enclosure of the trigeminofacial chamber by prootic and pterosphenoid. Most differences between early and late chirocentrids can be explained as evolutionary development common to several families of early teleosts. Characters in which *Chirocentrus* resembles clupeids must be viewed as having developed in parallel.

Relationships of elopoids, chirocentroids and clupeoids are shown in Figure 4. The few branches indicated in each suborder represent the several families which belong to each lineage. Thus, the chirocentroid line includes chirocentrids and saurocephalids whose derivation from chirocentrids was demonstrated in the section on "Evolution of Chirocentrid Fishes." The Elopoidea include elopids, pachyrhizoids, and albulids. Clupeoidea embrace clupeids, clupavids, and dussu-

mierids. Chanids are perhaps associated with the clupeoid group but this family may be more closely related to a pholidophorid derivative.

Whether the Leptolepidae should be included among teleosts or holosteans has been and remains a moot point. Many paleontologists (Berg, 1940; Dunkle, 1940; Romer, 1945; Schaeffer, 1947) include leptolepids in the superorder Teleostei but others (Erasmo, 1956; Saint-Seine, 1949; Arambourg & Bertin, 1958; Gardiner, 1960) place this family among the halecostomes, an intermediate group structurally transitional between holosteans and teleosteans. Leptolepids and several teleostean families share a common pattern of neurocranial and jaw structures. But leptolepids retain certain halecostome characters, including presence of a rostral, presence of a suborbital (in at least one species), a paleoniscoid arrangement of neurocranial sensory canals, ganoine cover on scales and head bones, and a large notochordal canal.

Because leptolepids may be assigned to one of two structural grades of actinopterygian fishes, the distinction between holostean or halecostome (if that category is used) and teleostean fishes cannot be drawn sharply. Early clupeiform fishes are derived from leptolepids or leptolepid ancestors, the pholidophorids. Thus, clupeiforms are monophyletic at the pholidophorid level. Including pholidophorids and leptolepids in the superorder Teleostei would make the teleosts a monophyletic category, but to call them teleosts would render this term meaningless in the sense that "teleost" is now used. Pholidophorids retain too many nonteleostean characters (Arambourg & Bertin, 1958; Rayner, 1948) to be included in the superorder Teleostei. If leptolepids are included among the teleosts, an important group is removed from the halecostomes. Without the leptolepids, the halecostome category would have to be abandoned. The two other orders presently included among the halecostomes, Pholidophoriformes and Aspidorhynchiformes, would have to be returned to the superorder Holostei, thus making holosteans a more diverse group than they already are. Therefore, I would retain the Halecostomi and exclude leptolepids from the teleosts.

SYSTEMATIC DESCRIPTIONS

Superorder TELEOSTEI Romer, 1945

Order CLUPEIFORMES Berg, 1940

Suborder CHIROCENTROIDEA Berg, 1940

Family CHIROCENTRIDAE Saint-Seine, 1949

Diagnosis. Elongate, clupeiform fishes. Body laterally compressed. Head length contained approximately 4-7 times in standard length. Neurocranium elongate. Supraoccipital, usually with a prominent crest, partly or completely separates parietals. Epiotic with enlarged dorsoposterior crest. Post-temporal fossa or groove present. Hyomandibular fossa conspicuous. Parethmoid with enlarged head for reception of palatine malleolus. Myodome canal present. Gape of mouth wide and direction of cleft terminal or upward. Upper border of mouth formed by premaxillary and maxillary but primarily the latter. Mandible elongate. Except in *Pachythrissops*, a single row of sharp teeth on each jaw. Teeth weakly ankylosed to jaws or in deep alveoli. No gular plate.

Vertebral centra ossified. Pleural ribs encircle body cavity. Epineural and epipleural intermuscular bones present. Narrow, elongate mesocoracoid. Scapula with saddle-shaped condyle for attachment of first pectoral fin ray. All fins present. Dorsal and anal fins remote from snout. Caudal fin deeply forked. Caudal fin rays segmented in oblique, stepwise fashion. First pectoral fin ray broad and elongate. Pectoral fin insertion low on body. Pelvic fin abdominal. Cycloid scales thin, commonly deciduous, ovate or dorsoventrally elongate.

Upper Jurassic-Upper Cretaceous.

Genus ALLOTHRISSOPS Nybelin, 1964

Allothrissops Nybelin, 1964, p. 16.

Type-species. Allothrissops salmoneus de Bdainville, 1818, p. 331.

Geologic occurrence and distribution. Kimmeridgian, Europe.

Diagnosis (emended). Elongate, slender fishes attaining a standard length of approximately 30 cm. Head longer than high and included 4.5-6.25 times in standard length. Supraoccipital crest developed. Parietals partly separated by supraoccipital. Post-temporal fossa present. Quadrate-mandibular joint below middle of orbit. Mouth cleft terminal. All jaws with single row of more slender and weaker teeth than in *Thrissops*. Coronoid process elongate but less sharply raised than in *Leptolepis*. Posteroventral area of preoperculum anterposteriorly expanded. Vertebrae 58-63, 31-35 abdominal, 26-29 caudal. Dorsal fin with 13-15 rays. Anal fin of 25-32 rays; anterior rays not enlarged.

Discussion. This diagnosis is expanded from data presented by Nybelin (1964) in order that diagnosis of Jurassic chirocentrids shall be of similar scope. The three species included in this genus are listed below. Data following each name are arranged thus: (1) author and source of original citation, (2) latest reviser, (3) species in syn-

onymy according to latest reviser, (4) geologic and geographic occurrence, (5) comments.

A. *Allothrissops salmoneus* (De Blainville): (1) De Blainville, 1818, p. 331; (2) Nybelin, 1964, p. 17; (3)—; (4) Kimmeridgian at Solnhofen and Eichstätt, Württemberg, West Germany; Cerin, Ain, France; (5) according to Nybelin, text-figure 116 of Saint-Seine (1949) pertains to *A. salmoneus* and not *Thrissops formosus*.

B. *Allothrissops mesogaster* (Agassiz): (1) Agassiz, 1833-1844, v. 2, pt. 2, p. 128, 165, 293; (2) Nybelin, 1964, p. 21; (3) ?*Thrissops cephalus* Agassiz, *T. micurus* Winkler, *T. clupeoides* Winkler, ?*T. salmoneus* var. *angustus* Wagner, ?*T. s.* var. *salmoneus* Wagner, *T. s. mesogaster* Wagner, ?*T. cephalus* Wagner; (4) Kimmeridgian at Eichstätt, Kelheim and Solnhofen, Württemberg, West Germany; (5) Relatively more common than *Allothrissops salmoneus;* Nybelin has identified 31 specimens.

C. *Allothrissops regleyi* (Thiollière): (1) Thiollière, 1854, pl. 10, fig. 2 (fig. only); (2) Nybelin, 1964, p. 26; (3) *Thrissops clupeoides* Woodward, 1895, p. 523; (4) Kimmeridgian at Cerin, Ain, France; (5) most common species of *Allothrissops*; Saint-Seine (1949) identified more than 300 specimens.

Nybelin (1964) cited a preoperculum (BMNH No. P. 45467) from the Bathonian (Middle Jurassic) near Oxford, England, which he believed corresponds in form and distribution of tubules of the preopercular sensory canal to this bone in the three species of *Allothrissops*. If properly assigned—and there seems no reason to doubt the generic relationship—this preoperculum represents the earliest chirocentrid and earliest teleost.

Genus THRISSOPS Agassiz, 1833

Thrissops Agassiz, 1833, v. 2, pt. 1, p. 12.
Type-species. Thrissops formosus Agassiz, 1833, p. 124, pl. 65a.
Geologic occurrence and distribution. Oxfordian-Cenomanian, Europe; Cenomanian, North Africa.

Diagnosis (emended). Elongate, slender or fusiform fishes probably attaining a standard length of 0.5 m. Head length included 4-6.5 times in standard length. Supraoccipital crest developed. Parietals partly or completely separated by supraoccipital. Post-temporal fossa present. Quadrate-mandibular joint below middle or anterior end of orbit. Mouth cleft directed upward. Premaxillary with short ventroposterior process. Premaxillary teeth longer than those of maxillary and stoutly conical. Maxillary dental border straight. Mandible without enlarged coronoid process. Dentary teeth of irregular size, the largest equal in height to those of premaxillary. Vertical and horizontal arms of preoperculum form right angle at posteroventral corner. Tubules of preopercular sensory canal confined to horizontal arm of preoperculum.

Vertebrae 56-63. Mid-lateral ridge of centra most enlarged of secondary strengthening ridges. Dorsal fin with 12-18 rays begins behind anal fin. Anal fin with 30-35 rays. Caudal fin strongly forked, internally heterocercal; 7-8 hypurals. Scales thin, circular or vertically elongate with fine circuli. No ganoine cover on scales or head bones.

Discussion. The emended diagnosis of *Thrissops* presented in this paper characterizes four species *(T. formosus, T. subovatus, T. microdon* and *T. vexillifer)* for which modern descriptions are available (Saint-Seine, 1949; Erasmo, 1946; Arambourg, 1954; Nybelin, 1964). More than 20 *Thrissops* species names are recorded in the literature but probably less than half are valid. Species retained in the genus according to latest revisers, as well as those *Thrissops* species which have not been mentioned since their original publication, are listed below in order of geologic occurrence. Data following each name are arranged in the same manner as for species of *Allothrissops*. Specimens assigned to *Thrissops* but of uncertain specific affinity are cited at the end of the species list.

A. *Thrissops costalis* (Egerton): (1) Egerton, 1845, p. 231; (2) Woodward, 1895, p. 528; (3)—; (4) Oxfordian at Christian Malford near Chippenham, Wiltshire, England; (5) only two specimens have been referred to this species.

B. *Thrissops formosus* Agassiz: (1) Agassiz, 1833, v. 2, pt. 1, p. 12, 1844, v. 2, pt. 2, p. 124, pl. 65a: (2) Nybelin, 1964, p. 5; (3) *T. heckeli* Thiollière; (4) Kimmeridgian at Kelheim and Solnhofen, Württemberg, West Germany; Cerin, Ain, France; Kimmeridge, England; (5) *T. formosus* is a common species; Saint-Seine (1949) and Nybelin have given measurements and fin ray counts of several individuals. The name *Thrissops propinquus* Woodward, 1895, p. 252 (BMNH No. P. 3683) appeared only on a specimen label until Woodward cited and assigned it to *T. formosus*.

C. *Thrissops subovatus* (Agassiz): (1) Agassiz, 1844, v. 2, pt. 2, p. 128; (2) Nybelin, 1964, p. 10; (3)—; (4) Kimmeridgian at Kelheim, Eichstätt, Württemberg, West Germany; (5)—.

D. *Thrissops rochei* Sauvage: (1) Sauvage, 1893, p. 436, pl. 8, fig. 2; (2)—; (3)—; (4) Kimmeridgian at Orbagnoux, France; (5) Present location of holotype and sole specimen unknown; validity of this species uncertain.

E. *Thrissops portlandicus* Woodward: (1) Woodward, 1895, p. 525, pl. 18, fig. 4; (2)—; (3)—; (4) Portlandian, Dorsetshire, England; (5) the holotype is the only specimen assigned to this species.

F. *Thrissops curtus* Woodward: (1) Woodward, 1919, p. 137, pl. 26, fig. 1; (2)—; (3)—; (4) Lower Purbeckian, Isle of Portland, Dorsetshire, England; (5) the holotype is the only specimen assigned to this species.

G. *Thrissops volgensis* Koslov: (1) Koslov, 1928, p. 573, pl. 41; (2)—; (3)—; (4) Lower Volgian (=Portlandian) near Gorodische, Government of Ulyanovsk, USSR; (5) if actually a *Thrissops*, this is the easternmost representative of the genus; only the holotype, an incomplete and poorly preserved specimen is known.

H. *Thrissops microdon* (Heckel): (1) Heckel, 1849, p. 18; (2) Erasmo, 1946, p. 45; (3)—; (4) Barremian at Tolfa, Italy; Albian, Pietraroia, Italy; Cenomanian; Isle of Lesina, Yugoslavia; Crespano, Comen, Gorizia, Italy; (5) relatively less numerous than *T. formosus*, specimens of *T. microdon* are more common than those of other nominal species of *Thrissops* from the Cenomanian. *Thrissops forcipatus* Bassani, 1879, p. 164, from Lesina, was placed in *T. microdon* by Bassani, 1882, p. 210.

I. *Thrissops gracilis* (Heckel): (1) Heckel, 1849, p. 18; (2) Erasmo, 1946, p. 50; (3)—; (4) Cenomanian at Comen, Italy; (5) *T. gracilis* (Heckel) is preoccupied by *T. gracilis* Giebel (1848, p. 151). Whether *T. gracilis* (Heckel) is distinct from *T. microdon* is uncertain.

J. *Thrissops exiguus* Bassani: (1) Bassani, 1879, p. 163; (2)—; (3)—; (4) Cenomanian, Isle of Lesina, Yugoslavia; Comen, Italy; (5) dubious species founded on a few small, fragmentary and contorted individuals, perhaps synonymous with *T. microdon*.

K. *Thrissops vexillifer* (Heckel): (1) Heckel, 1856, p. 245, pl. 2, fig. 1, 2; (2) Arambourg, 1954, p. 46; (3)—; (4) Cenomanian at Comen, Yugoslavia; Jebel Tselfat, Morocco; (5)—.

L. Fossils referred to *Thrissops* but of uncertain specific affinity include (1) *T.* aff. *regleyi* Sauvage, 1893, p. 438, Kimmeridgian at Bugey, France; (2) *T. latus* Wagner, 1863, p. 735 *(nom. dub.)*, Kimmeridgian at Eichstätt, West Germany; (3) *T.* sp. Woodward, 1889, p. 455, Kimmeridgian, Dorsetshire, England; (4) *T.* sp. Felix, 1891, p. 194, pl. 30, fig. 10. Cretaceous, Tlaxiaco, Mexico; (5) *T.* sp. Erasmo, 1922, p. 66, Mid-Cretaceous, ?locality.

Genus PACHYTHRISSOPS Woodward, 1919

Parathrissops Eastman, 1914, p. 423. (Name preoccupied: *Parathrissops* Sauvage, 1878, p. 629).

Pachythrissops WOODWARD, 1919, p. 128.
Type-species. Pachythrissops propterus (WAGNER), 1863, p. 735.
Geologic occurrence and distribution. Kimmeridgian, West Germany.

Diagnosis. Plump, fusiform fishes reaching standard length of 25 cm. Head length contained approximately 4 times and maximum depth of trunk included approximately 3 times in standard length. Mandibular articulation below middle of orbit. Premaxillary elongate, slender, with several rows of small, conical teeth. Maxillary slender, elongate; dental border convex with a single row of small teeth. Elongate, sharply raised coronoid process arises midway along mandibular length. Dentary teeth near symphysis enlarged; more posterior teeth as on maxillary. Vertebrae 50-54, 24-25 caudal. Centra with several, slender, longitudinal lateral ridges and grooves; mid-lateral ridge strongest, especially on caudal centra. Dorsal fin of 17-18 rays originates in front of anal fin. Anal fin with 20-22 rays exhibits anteriorly falcate profile. Pelvic fin arises at start of posterior third of distance from pectoral fin base to origin of anal fin. Scales thin, cycloid, with fine circuli.

PACHYTHRISSOPS PROPTERUS (Wagner), 1863

See synonymy in NYBELIN (1964).
Holotype. Complete fish in part and counterpart. Kimmeridgian at Eichstätt, West Germany (Munich, Universitäts-Institut für Paläontologie und historische Geologie, no. AS I 603).
Geologic occurrence and distribution. Kimmeridgian at Solnhofen, and Eichstätt, Württemberg, West Germany.

Diagnosis. Same as for genus.

Discussion. Two English species, *Pachythrissops laevis* and *P. vectensis* which WOODWARD (1919) assigned to *Pachythrissops*, differ from *P. propterus* in body proportions, structure of neurocranium, form of dentition, number of vertebrae, and relative positions of dorsal and anal fins. I believe that when these English fossils are restudied they will be assigned to a new genus. The two species named by WOODWARD are from middle Purbeck beds near Swanage, Dorsetshire, and Wealden deposits at Atherfield, on the Isle of Wight.

NYBELIN (1964) suggests that because *Pachythrissops* exhibits (1) several rows of fine premaxillary teeth, rather than a single row, (2) several fulcral scales anterior to the dorsal lobe of the caudal fin, rather than no such scales, and (3) other unspecified characters, *P. propterus* may be an ancestor of *Tarpon*. These two characters, as well as the gular plate illustrated (pl. 9, fig. 4) but not mentioned in the text, could serve to remove *Pachythrissops* from the chirocentrids. Intensive examination of the *Pachythrissops* neurocranium is required prior to such a move.

Genus MESOCLUPEA Ping & Yen, 1933

Mesoclupea PING & YEN, 1933, p. 269; CHANG, 1963, p. 105.
Type-species. Mesoclupea showchangensis PING & YEN, 1933, p. 270, pl. 1, fig. 1.
Geologic occurrence and distribution. Late Jurassic? (See section on "Geologic and Geographic Distribution"). China.

Diagnosis. See CHANG, 1963, p. 114.

Discussion. When originally described, *Mesoclupea* was assigned to the Clupeidae. CHANG reassigned this genus to the Chirocentridae because (1) the supraoccipital partly separates parietals, (2) the otic region is relatively prominent, (3) the snout is short, (4) gape of mouth is directed slightly upward, (5) no gular plate occurs, (6) the sensory canal system of the head has a teleostean pattern, (7) vertebral centra are well ossified, (8) the dorsal fin with short base arises behind the elongate anal fin, and (9) the pectoral fin is elongate and the pelvic fin small. CHANG compared *Mesoclupea* and *Thrissops* to support his opinion that *Mesoclupea* was a chirocentrid. *Mesoclupea* differs in several important particulars from *Thrissops*. The low supraoccipital crest and confinement of the supraoccipital to the median dorsoposterior corner of the neurocranium recalls leptolepids, rather than *Thrissops* or other chirocentrids. An epiotic crest is not developed. The dorsal surface of the neurocranium is nearly flat. Anterior to the orbit the head profile drops sharply, rather than following a straight line to the tip of the snout. The mouth cleft lies in a horizontal position, rather than being angled upward as in *Thrissops*.

In addition to the characters cited by CHANG, chirocentrid affinity is supported by several other characters. The parethmoid is enlarged. Vertical and horizontal arms of the preoperculum form a right-angled junction posteroventrally. In this latter character *Mesoclupea* resembles *Thrissops* and differs from other Mesozoic teleosts.

MESOCLUPEA SHOWCHANGENSIS, Ping & Yen, 1933

Mesoclupea showchangensis PING & YEN, 1933, p. 270, pl. 1, fig. 1; CHANG, 1963, p. 106, 3 pls., 2 figs.
Mesoclupea globicephala PING & YEN, 1933, p. 272, pl. 1, fig. 2; CHANG, 1963, p. 106.
Holotype (neotype, CHANG, 1963). Complete fish. Late Jurassic? from Showchang, Chekiang Province, China (Peking, Institute of Vertebrate Paleontology and Paleoanthropology, no. V. 2685.13).
Geologic occurrence and distribution. Late Jurassic? from Showchang, Linhai, Chuki, Chunan and Kienteh, Chekiang Province, Chungan, Yungan, Fukien Province, and Taihu, Kiangsi Province, China.

Diagnosis. See CHANG, 1963, p. 114.

Genus SPATHODACTYLUS Pictet, 1858

Spathodactylus PICTET, 1858, p. 2.
Type-species. Spathodactylus neocomiensis PICTET, 1858, p. 2, pl. 1.
Geologic occurrence and distribution. Neocomian, Switzerland.

Diagnosis (emended). Elongate, robust fish. Head length contained more than 5 times in standard length. Maximum depth of trunk exceeding length of head. Maxillary elongate, alveolar border nearly straight. Alveolar border of mandible weakly sinuous. Single row of stout, conical teeth on each jaw. Teeth on mandible slightly larger than teeth on upper jaw. Preoperculum with narrow vertical arm and broad, anteroposteriorly extended horizontal arm. Lateral surface of preoperculum smooth. Vertebrae 60(?); approximately 28 abdominal, 32 caudal; centra with single, lateral, longitudinal ridge. Short dorsal fin located above middle of anal fin. Anal fin falcate in profile; composed of approximately 30 rays. Pectoral fin formed of 6 short, distally expanded rays. Pelvic fin

formed of 4 broad rays. Scales large, oval with conspicuous circuli.

Discussion. Woodward (1901, p. 98) presented a diagnosis of this genus. The revised definition of *Spathodactylus* given above is based on data from the original description of the genus, the short account offered by Woodward, and examination of a photograph of the single, almost complete specimen in part and counterpart for which the name *Spathodactylus* was established. The head of this specimen is poorly preserved.

Saint-Seine (1949) suggested that *Spathodactylus* differed from *Chirocentrites* only in having smaller premaxillary teeth. The premaxillary of *Spathodactylus* may not be preserved (Woodward, 1901, p. 99; Pictet, 1858, p. 4). Pictet distinguished *Spathodactylus* from *Chirocentrites* because of its (1) straight maxillary dental border, (2) dentition of approximately uniform size, (3) anterior dorsal fin formed of a single ray, (4) unserrated opercular-subopercular contact, and (5) broad paired fins. These two genera do differ in characteristics (1) and (2); character (3) represents a displaced ray of the single posterior dorsal fin (Bassani, 1882). The nature of the opercular-subopercular contact can be determined only on well-preserved specimens. This region is not adequately preserved in *Spathodactylus*. Paired fins of *Spathodactylus* and *Chirocentrites* are broad. *Spathodactylus* is a Neocomian fish. *Chirocentrites* first appears in the Albian. Until more adequate material of *Spathodactylus* is available and the holotypes of both genera are restudied it seems wise to retain them as separate taxa.

The single species, *Spathodactylus neocomiensis* Pictet, is 76 cm. in standard length and comes from Voirons, Switzerland. Bassani (1882) questionably referred an incomplete fish from Cenomanian exposures on the Isle of Lesina, Yugoslavia, to this species.

Genus CHIROCENTRITES Heckel, 1849

Chirocentrites Heckel, 1849, p. 17.
Andreiopleura Costa, 1864, p. 97.
?*Heterolepis* Costa, 1865, p. 4.
Type-species. Chirocentrites coroninii Heckel, 1849, p. 17.
Geologic occurrence and distribution. Albian-Cenomanian, Italy and Yugoslavia.

Diagnosis. Elongate fishes, head and anterior part of trunk deep. Body tapering posteriorly to narrow peduncle. Head length contained approximately 6 times in standard length and less than greatest depth of trunk; head profile blunt. Two premaxillary teeth, each more than 1 cm. long, point ventroanterior, as in *Chirocentrus* and *Xiphactinus*. Maxillary broad, elongate, dental border sinuous; 29-30 teeth. Dentary teeth stoutly conical. Mandibular articulation situated below anterior border of orbit. Mouth cleft directed upward. Preoperculum with narrow vertical and long horizontal arm. Several ridges and grooves on central part of horizontal arm. Vertebrae 62, 33 abdominal and 28 caudal. Abdominal centra with two longitudinal, lateral ridges; caudal centra with one. Pleural ribs present on all but first 3 abdominal centra. Dorsal fin of 15 rays begins behind middle of anal fin. Anal fin with at least 34 rays; profile falcate. Pectoral fin with 5 rays; first ray broad and heavy. Pelvic fin originates at start of last third of distance between pectoral fin base and beginning of anal fin.

Discussion. The holotype of the single species, *Chirocentrites coroninii,* which is also the sole complete specimen, has not been restudied since Heckel (1850) described the genus. Additional body and fin fragments referred to *Chirocentrites* have been reported in subsequent studies (Erasmo, 1915, 1946; Bassani, 1882). This diagnosis therefore is drawn essentially from the description of Heckel. The holotype, from the Cenomanian of Gorizia, Italy, measures 53 cm. in standard length. Other, incomplete, specimens referred to this species have been obtained from Albian rocks at Pietraroia, near Benevento, Italy (Erasmo, 1915), and Cenomanian exposures on the Isle of Lesina (Bassani, 1882).

Genus EUBIODECTES Hay, 1903

Eubiodectes Hay, 1903b, p. 415.
Type-species. Chirocentrites libanicus Pictet & Humbert, 1866, p. 123, pl. 13.
Geologic occurrence and distribution. Late Cenomanian, Lebanon.

Diagnosis. Elongate, slender-bodied fishes. Premaxillary with stout, conical teeth. Maxillary and dentary teeth of approximately equal size, slender and closely spaced. Vertebrae ?60. Dorsal fin with 12-15 rays arising above middle or last third of anal fin, which has approximately 35 rays and falcate profile. Pectoral rays expanded distally, longitudinally divided.

Discussion. All specimens referred to this monotypic genus are incomplete. No complete head is preserved. In consideration of the elongate body shape Pictet & Humbert (1866) placed *Eubiodectes libanicus* in *Chirocentrites*. Bassani (1882) suggested that vertebral apophyses, appendages, and ribs of this species resembled those of *Thrissops microdon*. Woodward (1901) placed the Pictet & Humbert species in *Ichthyodectes* because of the close spacing and uniform size of the dentition. Hay (1903b) erected the generic name *Eubiodectes* for the same species. He distinguished the new genus as follows: (1) in *E. libanicus* the anterior ray of the pectoral fin expands distally and is divided longitudinally, whereas in *Ichthyodectes* the first ray is neither expanded nor divided: (2) a notochordal perforation of the centrum exists in *Eubiodectes* but is lacking in *Ichthyodectes*; (3) the anal fin of *Eubiodectes* is longer than that of *Ichthyodectes*. Examination of *Ichthyodectes* specimens demonstrates that the first pectoral fin ray is divided longitudinally and a small notochordal canal does persist. There are approximately 35 anal fin rays in *Eubiodectes* but less than a dozen in *Ichthyodectes*. In the large number of anal fin rays, *Eubiodectes* resembles *Thrissops*.

The affinities and taxonomic validity of *Eubiodectes* are still uncertain. Pending discovery of better specimens and restudy of available material, I believe that this genus should be retained, at least for reasons of its geographic separation from other chirocentrid fishes. It may be shown eventually that *E. libanicus* is a species of *Thrissops*. Specimens of this species come from the late Cenomanian at Mt. Hakel and Mt. Hajula, Lebanon.

Genus PROPORTHEUS Jaekel, 1909

Proportheus JAEKEL, 1909, p. 396.
Type-species. Proportheus kameruni JAEKEL, 1909, p. 396, pl. 1.
Geologic occurrence and distribution. Turonian or Senonian, Cameroun Republic and Spanish Guinea.

Diagnosis. Elongate, shallow-bodied fish. Greatest depth of body equal to length of head and contained about 5.5 times in standard length. Head longer than high. Mandibular articulation below middle of orbit. Direction of mouth cleft upward. Premaxillary slightly longer than high; first tooth enlarged and projecting ventroanteriorly. Maxillary with numerous short, conical teeth, resembling that of *Chirocentrus*. Elongate, broad groove on ventrolateral surface of mandible. No coronoid process. Mandibular teeth larger than those on maxillary. Ventroposterior border of preoperculum curved. Lateral surface of preoperculum with about a dozen grooves extending posteriorly and ventrally. Perhaps 60 centra in complete specimen. Dorsal fin arising just posterior to origin of anal fin. At least 30 anal fin rays. Pectoral fin robust, first two rays flat, divided distally. Pelvic fin closer to anal than to base of pectoral fin.

PROPORTHEUS KAMERUNI Jaekel, 1909

Plate 2, figure B

Proportheus kameruni JAEKEL, 1909, p. 393, pl. 1.
Chirocentrites? guinensis WEILER, 1922, p. 149.
Holotype. Head and several anterior vertebrae, Turonian or Senonian, Mamfe, Cameroun Republic. The type, formerly at the Geologischen Landesmuseum in Berlin, is probably in the USSR (Dr. GROSS, personal communication).
Geologic occurrence and distribution. Turonian or Senonian, Mamfe, Cameroun Republic; Ibando, San Benito River, Spanish Guinea.

Diagnosis. Same as for genus.

Description. No complete specimen is known. Study of an individual (AMNH No. 6302) exhibiting an almost complete head and trunk but lacking unpaired fins provides additional information on the structure of *Proportheus*. Body outline and proportions are indicated in the generic diagnosis. The prognathic head, a little longer than high, resembles that of the holotype. The supraoccipital crest is higher and longer than in *Thrissops*. A weak epiotic crest is developed. The dorsal surface of the frontals is flat. Snout length approximately equals orbit length, which in turn slightly exceeds postorbital length of the neurocranium. The parethmoid has a stout discoidal head directed ventroanteriorly. This head is relatively larger than in *Thrissops*.

The premaxillary measures approximately 1.5 cm. long and 1 cm. high. Its dental border is lined with conical teeth. The forwardmost tooth, at least 7 mm. in length, is directed ventroanteriorly. The 7 cm. long, narrow maxillary is gently curved and about as broad as the first pectoral fin ray. In outline the maxillary resembles that of *Chirocentrus*. Approximately a dozen, 2-3 mm. long, sharp, conical teeth line the anterior part of the maxillary. Posterior maxillary teeth are short and blunt. The mandible, almost 8 cm. long, increases in height posteriorly from the 1.5 cm. high symphysis. There is no coronoid process. A longitudinal groove appears on the ventrolateral half of the mandible arising just behind the symphysis and extending to the posterior border of the lower jaw. The quadrate-mandibular articulation lies below the middle of the orbit and the lower jaw is inclined sharply upward. A stout palatine malleolus is present. The preoperculum has a gently curved, ventroposterior border. Approximately 9 grooves and ridges line the ventrolateral surface. The preoperculum of the holotype exhibits a dozen such grooves.

Fifty-eight centra are preserved on AMNH no. 6302. Abdominal centra are a little higher than long whereas caudal centra are of equal height and length. Ribs are stout and medially grooved. WEILER (1922) stated that the dorsal fin, arising just posterior to the start of the anal fin, was composed of 10-11 rays. There are 30 anal pterygiophores on AMNH no. 6302. The pectoral fin has 7-9 rays. The broad first ray is 9 cm. long and longitudinally divided distally. The second ray, like the first, is broad and divided distally. The remaining rays are narrower. The pelvic fin arises closer to origin of the anal fin than to base of the pectoral fin. Scales on the holotype are round with numerous circuli.

Discussion. JAEKEL described a bone lying below the mandible as a splenial. Teleosts lack a splenial. This "bone" is actually the lower margin of the dentary which appears to have separated from the rest of the mandible on the crushed holotype.

Genus CLADOCYCLUS Agassiz, 1841

Cladocyclus AGASSIZ, 1841, p. 83.
Anaedopogon COPE, 1871b, p. 53.
Chiromystus COPE, 1885, p. 4.
Ennelichthys JORDAN, 1921, p. 80.
Type-species. Cladocyclus gardneri AGASSIZ, 1841, p. 83.
Geologic occurrence and distribution. Late Cretaceous, Brazil.

Diagnosis. See SANTOS, 1950, p. 128.

Discussion. SANTOS (1950) revised the genus *Cladocyclus*. Numerous fragments, primarily scales, from England, continental Europe, North America, and Australia were referred to *Cladocyclus* in the 19th and 20th centuries. These specimens belong to other families (see section on "Species Formerly Considered Chirocentrids") or other chirocentrid genera (see *Ichthyodectes*).

The following species are included in *Cladocyclus* according to SANTOS (1949, 1950).

C. gardneri AGASSIZ. Late Cretaceous, Barra do Jardim, Crato and neighboring localities in Ceará.
C. ferus SANTOS. Late Cretaceous, Sitio do Romualdo, Crato, Ceará.
C. woodwardi (SANTOS). Late Cretaceous, Manguinhos, Itaparica Island, Bahia.
C. mawsoni (COPE). Late Cretaceous, eastern shore of Todos os Santos Bay, near Agua Comprida, and Itaparica Island, Bahia.
C. alagoensis (JORDAN). Late Cretaceous, Riacho Doce. Alagoas.

Genus PRYMNETES Cope, 1871

Prymnetes COPE, 1871b, p. 52.
Type-species. Prymnetes longiventer COPE, 1871b, p. 52.
Geologic occurrence and distribution. Geologic position uncertain (see section on "Geologic and Geographic Distribution"): Chiapas, Mexico.

Diagnosis. Elongate, slender-bodied fishes. Head length contained almost 5 times in standard length and slightly exceeding maximum depth of trunk. Maxillary resembling that of *Gillicus*. Mouth cleft directed upward. Mandible with elongate, broad, ventrolateral groove as in *Cladocyclus*. Vertebrae approximately 75, 50 abdominal and 25 caudal. Centra with strong lateral ridge. Abdominal centra about as high as long, caudal centra longer than high. Dorsal fin of ?12 rays. Pectoral fin robust, first ray broad and flat. Pelvic fin arising close to anal fin. Scales dorsoventrally elongate, with numerous circuli and several anterior radii.

Discussion. COPE suggested that *Prymnetes* was an elopid because its "body shape, interneural spines, normal and supernumerary ribs" resemble these structures in *Elops* and *Megalops*. These ill-defined features are common to all early teleosts. WOODWARD (1901) suggested that *Prymnetes* might be a chirocentrid but gave no reason for his supposition. Assignment of *Prymnetes* to the Chirocentridae is supported by its (1) elongate body, (2) mouth cleft directed upward, (3) shape of maxillary similar to that of *Gillicus*, (4) centra with stout longitudinal, lateral ridge, (5) posterior location of dorsal fin, and (6) robust pectoral fin.

PRYMNETES LONGIVENTER Cope, 1871
Plate 1, figure B

Prymnetes longiventer COPE, 1871b, p. 52.
Holotype. Almost complete fish lacking anal fin. ?Cretaceous, Tuxtla (presumably Tuxtla Guiterrez), Chiapas, Mexico. Washington USNM no. 4090 (original no. 9819).
Geologic occurrence and distribution. Only holotype known.

Diagnosis. Same as for genus.

Discussion. The head of the holotype is distorted. Therefore standard length cannot be measured precisely; the measurement is more than 40 but less than 45 cm. COPE mistook for the dorsal fin a part of the upper lobe of the caudal fin which is bent forward over the body. At least 20 anal fin rays are present, as determined by count of anal pterygiophores.

Genus XIPHACTINUS Leidy, 1870

Megalodon AGASSIZ, 1835, p. 55 (*non* SOWERBY, 1829) (*nom nud.*).
Hypsodon AGASSIZ, 1837, p. 104.
Xiphactinus LEIDY, 1870, p. 12.
Portheus COPE, 1871c, p. 175.
Type-species. Xiphactinus audax LEIDY, 1870, p. 12.
Geologic occurrence and distribution, Albian-Santonian, England and Europe; Cenomanian-Campanian, North America; Upper Cretaceous, Australia.

Diagnosis. Elongate fishes attaining a standard length of more than 4 m. Maximum body depth contained about 5.5 times in standard length. Head length contained 5.5-6 times in standard length and about equal to maximum depth of trunk. Supraoccipital crest forms one-third of neurocranial height. Parietals fused at midsagittal line. An elongate cluster of small knobs on parietals at midline. Basipterygoid process prominent. Mean angle between otic and orbital sections of parasphenoid 160 degrees. Ventral surface of parasphenoid gently convex. Intercalar forms part of lateral and posterior face of hyomandibular fossa. Development of subtemporal fossa as in *Tarpon*. Mean number of premaxillary alveoli 2.6 (range 2-5). Premaxillary teeth ventroanteriorly directed; one tooth may reach 6 cm. in crown height. Mean length of maxillary alveolar border 20 cm. Mean number of maxillary alveoli 33 (range 22-39). Stout, conical maxillary teeth of irregular size. Mandibular symphysis included 2.0-2.9 times in length of mandibular alveolar border. Mean number of dentary alveoli 22 (range 16-25). Dentary teeth of irregular size. Vertebrae 85-89, 52-57 abdominal, 29-33 caudal. Centra with stout, longitudinal, lateral ridge between two deeply incised longitudinal grooves. Dorsoventral height of this ridge twice width of groove opening. Dorsal fin of 15 rays; length of dorsal fin base included approximately twice in its maximum height. Anal fin with 12-14 rays located in front of dorsal fin. Anal fin base contained twice in maximum height of anal fin. Pectoral fin with 8-9 rays. First ray undivided, forming broad saber-shaped blade. Pelvic fin arising in posterior quarter of distance between pectoral fin base and origin of anal fin. Mid-body scales 4-5 cm. high and 2-3 cm. long. Few centrally located, short anterior radii on scales behind head; none on mid-body scales. Minute, irregularly spaced punctae on posterior half of scales.

Discussion. Four names have been applied to this genus. AGASSIZ (1835) first called it *Megalodon*, but two years later, noting that this name had been used by SOWERBY for a mollusk, substituted *Hypsodon*. Several genera were included in *Hypsodon*. By priority *Hypsodon* should apply to a pachyrhizodid, for the first specimen mentioned by AGASSIZ when he described the single species of *Hypsodon* is the pachyrhizodid that WOODWARD (1901) named *Thrissopater magnus*. COPE (1875) recognized that AGASSIZ had included more than one kind of fish in *Hypsodon* and proposed to distinguish under the name *Portheus* specimens resembling a fish which he had described in 1871. LEIDY (1870) named an incomplete pectoral fin ray *Xiphactinus audax*. This specimen is identical with fin rays which COPE assigned to *Portheus*. Therefore, *Xiphactinus,* although less well known than *Portheus*, is, by priority, the valid name for this fish. Because the relatively few specimens referable to *Xiphactinus* from outside of North America are incomplete, the above generic diagnosis is based essentially on North American material.

XIPHACTINUS AUDAX Leidy, 1870
Plate 1, figure A; Text-figures 5-12, 13, *A, B*

Xiphactinus audax LEIDY, 1870, p. 12; COPE, 1872a *(?Xiphactinus)*, p. 341, 348; LEIDY, 1873, p. 290, 348, pl. 17, fig. 9-10; COPE, 1875, p. 276; STEWART, 1898b, p. 115; STEWART, 1900, p. 267, pl. 33-39, 41-45A, 46-47B, fig. 1; BUMP, 1926, p. 99, 3 fig.; STOVALL, 1932, p. 87, pl. 9.
Saurocephalus audax COPE, 1870, p. 533; COPE, 1871a, p. 415, 418.
Saurocephalus thaumas COPE, 1870, p. 533; COPE, 1871a, p. 418, 422.
Portheus molossus COPE, 1871c, p. 175; COPE, 1872a, p. 324, 338, 342; COPE, 1872b, p. 328, 333; COPE, 1874, p. 39; COPE, 1875, p. 50, 183, 273, pl. 39, 40, figs. 1-9, pl. 41, 44, figs. 5, 10-11, pl. 45, fig. 9-11; WOODWARD, 1901, p. 92; WOODWARD, 1913, p. 529, pl. 18; THORPE, 1934, p. 121, 2 figs.
Portheus thaumas COPE, 1872a, p. 342; COPE, 1872b, p. 333, 335;

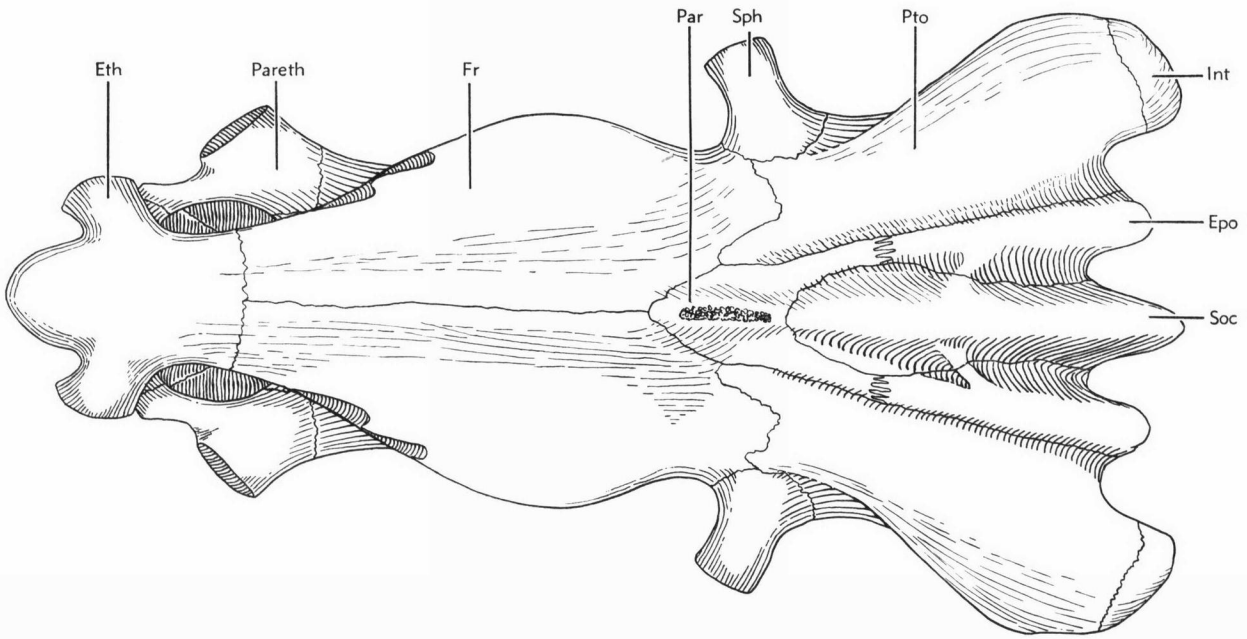


FIGURE 5. *Xiphactinus audax* LEIDY. Restoration of dorsal aspect of neurocranium. Based on KU No. 262, ×0.5. [For explanation of abbreviations see p. 4.]

COPE, 1874, p. 40; COPE, 1875, p. 196, 273, pl. 43, fig. 1-4, pl. 44, fig. 1-4; COCKERELL, 1908, p. 173.

Portheus lestrio COPE, 1873, p. 338; COPE, 1875, p. 201, 274, pl. 42, fig. 1-3, pl. 47, fig. 1.

Portheus mudgei COPE, 1874, p. 40; COPE, 1875, p. 203, 273.

Portheus lowii STEWART, 1898a, p. 24, pl. 2, fig. 2.

Xiphactinus molossus STEWART, 1898b, p. 116.

Xiphactinus thaumas STEWART, 1898b, p. 116.

Xiphactinus brachygnathus STEWART, 1899, p. 107; STEWART, 1900, p. 293, pl. 45, fig. 3-4.

Xiphactinus lowii STEWART, 1900, p. 293, pl. 48, fig. 2.

Holotype. Incomplete first pectoral fin ray, Niobrara Formation, Smoky Hill River, Kansas. USNM No. 52.

Geologic occurrence and distribution (see list of material examined for speecific localities). Greenhorn Limestone, Kansas; Carlile Shale, Kansas, Nebraska; Eagle Ford Shale, Texas; Austin Chalk, Texas; Niobrara Formation, Kansas, Nebraska; Selma Chalk, Alabama, Arkansas; Vermilion River Formation, Manitoba.

Diagnosis. Essentially same as for genus (see discussion of *Xiphactinus audax*). Mean ratio of maxillary height at palatine condyle to length of alveolar border, 43. Profile of maxillary drops sharply behind palatine condyle. Palatine head of parethmoid projects ventroanteriorly.

Material examined. More than 200 specimens referable to *Xiphactinus audax* were seen. These include (1) more or less complete specimens on exhibit at several museums (Table 3), (2) intact heads or neurocrania and associated material, (3) isolated jaws, vertebrae, parts of pectoral and pelvic girdles, and fin rays. Heads and neurocrania, plus several jaws and vertebrae known from specific localities are listed below. All localities are in Kansas unless otherwise stated.

Greenhorn Limestone (probably Lincoln Limestone Member).

KU no. 561, Salt Creek, 4 mi. N. Gorham, Russell Co., postorbital part of neurocranium; MCZ no. 5401, 2 mi. NW Holyrood, Ellsworth Co., head; USNM no. 11121, T. 4 S., R. 4 W., Republic Co., mandibles.

Carlile Shale (Fairport Chalky Shale Member).

FH no. 11323, 4 mi. N. McCracken, Rush Co., head; KU no. 248, Fairbury, Jefferson Co., Nebraska, mandibles.

Eagle Ford Shale.

KU no. 594, at Bosqueville, NW of Waco, McLennan Co., Texas.

Austin Chalk.

USNM no. 18392, 7½ mi. SE Britton, Ellis Co., Texas, head.

Niobrara Formation (Smoky Hill Chalk Member).

Ellis Co.: AMNH no. 1706, T. 12 S., R. 20 W., neurocranium and jaws; KU no. 9820, sec. 5, T. 11 S., R. 20 W., scapula and vertebrae.——Gove Co.: AMNH no. 1747, T. 14 S., R. 26 W., maxillary, quadrate and vertebrae; KU no. 158, sec. 5, T. 13 S., R. 35 W., front of neurocranium, upper and lower jaws; KU no. 930, Martin's Canyon, T. 14 S., R. 26 W., neurocranium; CMNH no. 10421, sec. 16, T. 13 S., R. 26 W., neurocranium, jaws, hyopalatine, operculars, vertebrae and fin rays; AMNH no. 1673, head; AMNH no. 2373, neurocranium, jaws, operculars, palate; USNM no. 3782, neurocranium and jaws; USNM no. 11653, head.——Graham Co.: FH no. 8395, 3 mi. NW Bogue, head.——Jewell Co.: KU no. 11834, T. 3 S., R. 8 W., incomplete head.——Logan Co.: AMNH no. 8261, sec. 8, T. 12 S., R. 36 W., snout; AMNH no. 8590, E½ sec. 12, T. 15 S., R. 35 W., posterior end of neurocranium and premaxillary; USNM no. 11554, T. 15 S., R. 35 W., head; KU no. 320, head; KU no. 991, neurocranium; AMNH no. 1665, Fox Canyon (locality as cited by COPE, 1875), neurocranium and jaws; AMNH no. 8112, neurocranium.——Rooks Co.: AMNH no. 8115, sec. 5, T. 6 S., R. 17 W., upper and lower jaws.——Trego Co.: KU no. 245, sec. 16, T. 14 S., R. 25 W., upper and lower jaws, palate and vertebrae; KU no. 929, sec. 15, T. 14 S., R. 25 W., vertebrae; AMNH no. 2332, T. 15 S., R. 24 W., fin ray fragments; USNM no. 11178, W½ sec. 14, T. 11 S., R. 22 W., centrum; KU no. 735, 2(?) mi. NW Wakeeney, head; KU no. 9888, NW corner, SE¼ sec. 15, T. 14 S., R. 25 W., neurocranium; USNM no. 4207, near Wakeeney, neurocranium, jaws, palate.——Franklin Co., Nebraska: USNM no. 50, 041, NE¼ sec. 11, T. 1 N., R. 15 W., head and pectoral fins.——The following specimens, including several of the more completely preserved fishes, are from the Niobrara Formation of western Kansas but precise locality data are unknown: KU no. 124, neurocranium, partial palate and upper jaw; KU no. 160, neurocranium, jaws, preoperculum, vertebrae and pectoral girdle; KU no. 165, neurocranium, jaws, palate, vertebrae and pectoral girdle; KU no. 166, neurocranium, jaws, palate, vertebrae and pectoral girdle;

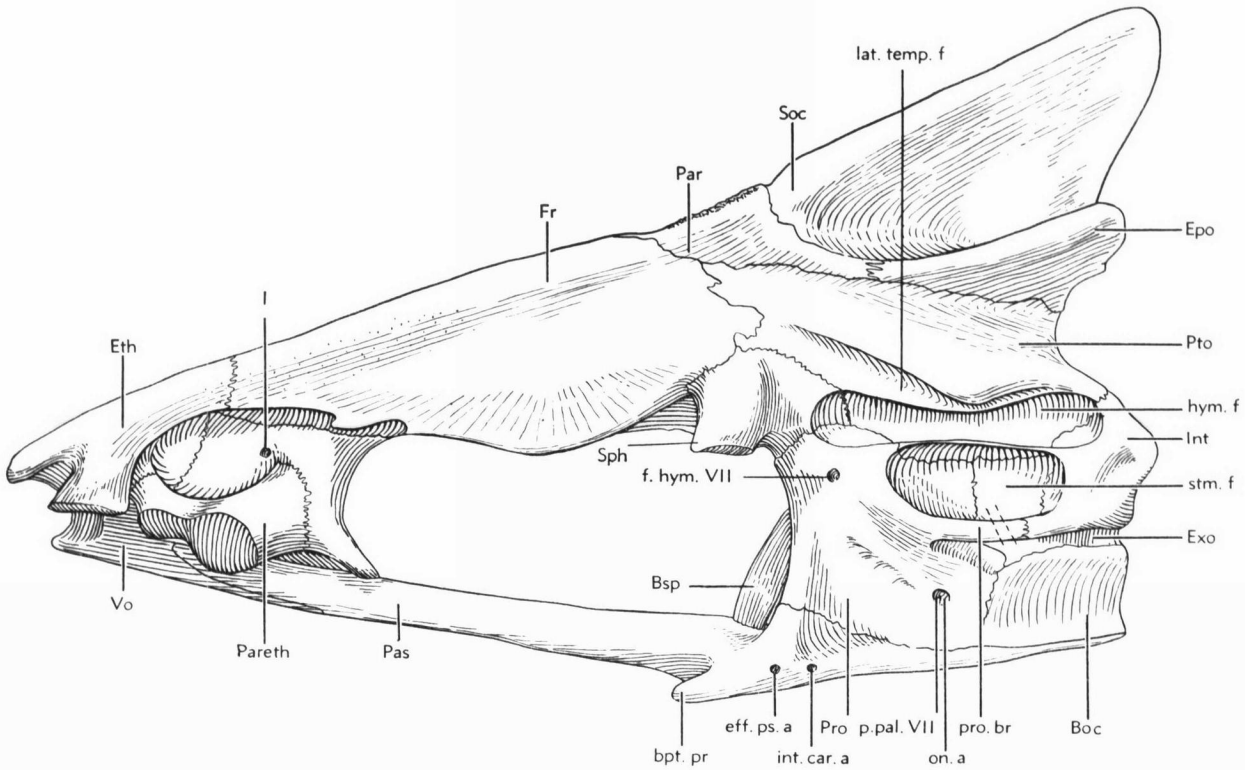


FIGURE 6. *Xiphactinus audax* LEIDY. Restoration of lateral aspect of neurocranium. Based on KU No. 262 and No. 124, ×0.5. [For explanation of abbreviations see p. 4.]

KU no. 168, neurocranium, jaws, palate, vertebrae and pectoral girdle; KU no. 183, neurocranium, jaws, operculars, hyopalatine elements and vertebrae; KU no. 262, neurocranium; KU no. 477, neurocranium, parts of mandible and palate; KU no. 565, postorbital part of neurocranium; KU no. 11661, head; KU no. 12011, neurocranium, upper jaw and part of palate; AMNH no. 1719, neurocranium, jaws palatal elements and pectoral girdle; AMNH no. 1732, head; AMNH no. 7382, neurocranium; AMNH no. 8272, neurocranium and jaws; USNM no. 1646, neurocranium; CM no. 1189, neurocranium and vertebrae; NMC no. 8152, head and anterior part of body; NMC no. 8152A, head and pectoral girdle.

Vermilion River Formation.

NMC no. 8799, sec. 4, T. 1 N., R. 2 W. of first meridian (near Altona, Manitoba) [location doubtful].

Description. [*Historical review.*] Several authors have contributed to the description of this genus. COPE (1875) combined and expanded his earlier reports on species of the genus *Portheus*. With limited material available, his description was incomplete. NEWTON (1877) provided an account of the English species, *Portheus gaultinus*. The single specimen which he reported upon is incomplete and the description inadequate for a thorough evaluation of differences between the North American and English species of *Xiphactinus*. CROOK (1892) gave a short description of *Portheus* from North America. His interpretation of neurocranial and postcranial structures included numerous errors. HAY (1898a) corrected misinterpretations of CROOK and COPE and provided a description of *Xiphactinus* with especial attention to the neurocranium. He compared *Xiphactinus* almost bone by bone with *Tarpon*. In several particulars he was unable to delimit certain bones such as parietals, did not describe others such as the vomer, and mistook the dorsal surface of the vertebrae for ventral. STEWART (1900) published detailed descriptions of *Xiphactinus* material in the Museum of Natural History at Kansas University. LOOMIS (1900) included a brief section on *Portheus*. OSBORN (1904) provided a short description of the first almost complete *Portheus* to be placed on display (AMNH no. 8443). MCCLUNG (1908) contributed descriptions of mandible, pectoral girdle and opercular bones of *Xiphactinus*. [See Table 3.]

[*Body form.*] *Xiphactinus* is the longest fossil teleost known. In length it exceeds any living isospondyl and matches that of living swordfishes. The elongate body (Pl. 1, fig. A) exhibits a straight dorsal line from head to dorsal fin. Posterior to the dorsal fin the body tapers toward the caudal fin base. The ventral profile of the head projects sharply downward from snout to pectoral fin. Behind this fin the ventral profile parallels the dorsal line up to pelvic fin insertion and then tapers to the caudal fin base. The body outline resembles that of *Chirocentrus dorab* and *Chirocentrites coroninii*.

None of the complete specimens depicts the outline of *Xiphactinus* exactly as in life. On the best-preserved individuals (FH no. 5026, DNHM no. 1667) the head arches only slightly upward. Others (USNM no. 21375) show both head and tail bowed dorsally. Opisthotonic distortion is frequently observed in fossil fishes. It is difficult to

TABLE 3. *Entire Individuals and Composite Specimens of Xiphactinus audax on Display or in Storage at Several Musems.*

Specimen	Locality and Formation	Specimen Condition and Remarks
AMNH 8443	Near Elkader, Logan Co., Kans. Niobrara Fm.	Specimen preserved in approximately natural position. Dorsal, part of anal and pectoral fins, pelvic fin and girdle restored. Standard length 401 cm. Total length 478 cm. Vertebrae 85: 57 abdominal, 29 caudal.
CM 4101, 4102	Logan Co., Kans. Niobrara Fm.	Composite of two individuals. Chirocentrid or saurocephalid centra and opercular fragments in abdomen.
CNHM, UF 973	Western Kansas Niobrara Fm.	Specimen opisthotonic. Unpaired fins restored. Standard length 370 cm. Vertebrae 85: 52 abdominal, 33 caudal.
DNHM 1667	sec. 24, T. 13 S., R. 28 W., Gove Co., Kans. Niobrara Fm.	Specimen preserved in approximately natural position. Part of caudal and anal fins restored. Standard length 383 cm. Vertebrae 85: 53 abdominal, 32 caudal. *Gillicus* vertebrae and head fragments in body cavity.
FH 5026	NE ¼, sec. 16, T. 13 S., R. 26 W. Gove Co., Kans. Niobrara Fm.	Most complete and best preserved individual. Standard length 418 cm. Total length 482 cm. Vertebrae 86: 56 abdominal, 30 caudal. Almost complete, intact *Gillicus* in abdominal cavity.
KU 103	Western Kansas Niobrara Fm.	Composite specimen. Pleural rib restoration excessively long.
UNSM 1495	?sec. 16, T. 15 S., R. 34 W. Berry Farm, Butte Creek, Logan Co., Kans. Niobrara Fm.	Body slightly sinuous. Dorsal and part of caudal fin restored. Standard length 350 cm. Vertebrae 89: 56 abdominal, 33 caudal. Vertebral fragments of enchodontid in body cavity.
Oakley, Kans. Public School 13-25	2½ mi. NE Monument Rocks, Gove Co., Kans. Niobrara Fm.	Composite specimen. Dorsal fin restored.
OUSM 1-0-S32	4 mi. NE Celina, Collin Co., Tex. Austin Chalk	Composite specimen. Caudal fin from *Cimolichthys*. Abdomen displaced sharply dorsad. Dorsal and pelvic fins restored.
YPM 2177	18 mi. SW Russell Springs, 35 mi. N Leoti, Logan Co., Kans. Niobrara Fm.	Specimen preserved essentially in natural position. Dorsal and parts of caudal fins restored. Standard length 395 cm. Vertebrae 87: 55 abdominal, 32 caudal.
SDSM 2510	6½ mi. SE Hot Springs, Fall River Co., S. Dak. Niobrara Formation.	Specimen lacks dorsal, anal and pelvic fins. Pleural rib restoration excessively long. Standard length 320 cm. Five shark teeth were found in abdominal cavity.
TMM 1837	3 mi. E Celina, Collin Co., Tex. Austin Chalk	Body arched gently upward. Extensive restoration of head, girdles and fins. Standard length approximately 325 cm.
SDNHM 63.02	Western Kansas Niobrara Fm.	Specimen slightly opisthotonic. Median fins restored; upper lobe of caudal fin incomplete. Standard length approximately 365 cm.
SDNHM 63.01	Western Kansas Niobrara Fm.	Caudal region twisted ventrally. All fins restored. Standard length 345 cm. Vertebrae 85: 52 abdominal, 33? caudal.
USNM 21375	4 mi. S and ¾ mi. E Savoy, Fannin Co., Tex. Austin Chalk (Ector Chalk Member)	Specimen strongly opisthotonic. Median fins in part restored. Vertebrae 87: 54 abdominal, 33 caudal. *Ananogmius* vertebrae in abdomen.

TABLE 3. *(Continued)*

Specimen	Locality and Formation	Specimen Condition and Remarks
USNM 11650	T. 15 S., R. 31 W. Gove Co., Kans. Niobrara Fm.	Vertebral column slightly sinuous. Anterior end of head missing. Right upper jaw placed in position of lower jaw. Dorsal and anal fins missing or incomplete. Vertebrae 87. *Gillicus* maxillary, vertebrae and other fragments in abdominal cavity.
NMC 8151	Gove Co., Kans. Niobrara Fm.	Composite specimen.
BMNH P. 11125	Western Kansas Niobrara Fm.	Composite specimen. Head from another individual.

determine maximum body depth because ventral ends of pleural ribs are not preserved on most individuals. In FH no. 5026 and DNHM no. 1667 maximum body length is contained 5.5 and 6 times, respectively, in standard length. The head, including operculum, of each of these two specimens is included 6 times in the standard length. On AMNH no. 8443, the head is contained 5.5 times in standard length. Examination of intact, relatively undistorted specimens of *X. audax*, comparison of these specimens with *Chirocentrus dorab* and other early clupeiforms indicates that the body of *X. audax* was slender in transverse section, rather than rounded as in *Tarpon atlanticus*.

[*Neurocranium.*] Lateral, or less frequently, dorsoventral compression has distorted *Xiphactinus* neurocrania. Nevertheless, the shape of this unit can be restored and most of the sutures followed. The elongate neurocranium is triangular in dorsal view (Fig. 5). Lateral projection of the ethmoid is less conspicuous, whereas that of the parethmoid is more pronounced than in *Chirocentrus*. The sphenotic has a stout, lateral process. The supraoccipital crest extends beyond the ventroposterior end of the neurocranium. A ridge formed by parietal and epiotic arises lateral to the supraoccipital crest and attains approximately one-third the height of this crest. The pterotic slopes posterolaterally from the base of the parietoepiotic ridge.

In lateral view (Fig. 6), the greatest neurocranial height is measured posteriorly where the supraoccipital crest comprises approximately one-third of neurocranial height. A subtemporal fossa excavated in the neurocranium is roofed by the pterotic, limited anteriorly and ventrally by the prootic, and posteriorly as well as ventrally by the exoccipital. Length of the orbit exceeds that of the postorbital section of the neurocranium. A medially directed depression in the ethmoid and parethmoid houses the nasal capsule. Measured from anterior end of the vomer to posterior end of the basioccipital, the mean neurocranial length of 26 specimens is 29 cm. (range, 20-37 cm.; standard deviation, 4 cm.).

The single vomer forms the ventroanterior end of the neurocranium. This bone is three times longer than wide. Beginning with a sturdy, anteriorly directed process, the vomer broadens posteriorly to form a pair of rounded, anteriorly directed facets. The anterior condyle on the dorsomedial surface of each maxillary abuts on these facets. Posterior to these facets for the maxillary, the vomer tapers in width and lies between anterior arms of the parasphenoid. Excavations on the ventral surface of the vomer posterior to the maxillary facets housed stout ligaments which anchored the palatine bones to the neurocranium. A series of small, rounded, bony prominences are situated along the mid-ventral line of the vomer.

The ethmoid (dermethmoid and mesethmoid) forms the foremost element of the neurocranium. In dorsal view, the ethmoid is rounded anteriorly. A stout process projects lateroventrally midway along the length of this bone. Posteriorly ethmoid and frontals meet in a zigzag suture. Two deep fossae separated by a mid-sagittal ridge appear below the anterior end of the ethmoid. Stout ligaments arose from the dorsal surface of each premaxillary and were inserted in each of these fossae. The lateroventral projection mentioned above bears a ventroanterior facet continuous with the maxillary facet of the vomer. In part, the anterior condyle of the maxillary also abuts on this ethmoid facet. Unless an unpreserved cartilaginous connection was present, the ethmoid does not meet the palatine posteroventrally. A deep pocket in the posterolateral face of the ethmoid houses the anterior section of the nasal capsule. A small bone observed in some specimens (KU no. 930, no. 9888, no. 11661, CMNH no. 10115), separated from the rest of the ethmoid by a wavy suture, lies in the anterior notch of the nasal capsule. This bone is probably a remnant of one of several separate ossification centers contributing to the ethmoid (SWINNERTON, 1902). MCCLUNG (1908) erroneously assigned to the vomer a section of the ethmoid which forms the anteromedial wall of the nasal capsule. In section, the dorsal surface of the ethmoid exhibits lamellar dermal bone while the mass of the ethmoid beneath this surface is composed of cancellous endochondral bone.

Paired parethmoids limit the orbit anteriorly, produce posterior and medial walls of each nasal capsule, and in the form of a round, hammer-like head project ventroanteriorly to meet each palatine. The suture separating endochondral and dermal elements of the parethmoid runs approximately dorsoventrally across the base of the palatine head and then curves inward toward the rear of the nasal capsule. Thus, the palatine head and medial wall of the nasal capsule are endochondral in origin, whereas the anterior wall of the orbit and posterior part of the nasal capsule are of dermal origin. The anterior wall of the orbit

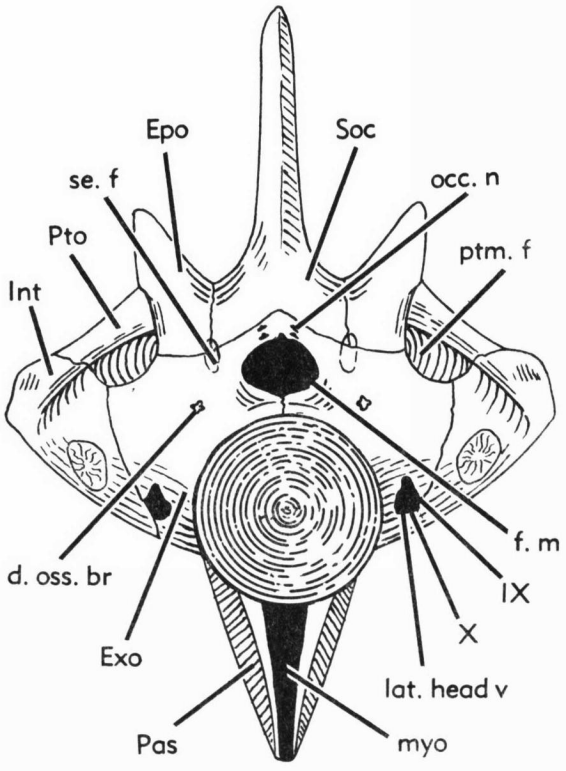


FIGURE 7. *Xiphactinus audax* LEIDY. Restoration of posterior aspect of neurocranium. Based on KU No. 738, ×0.5. [For explanation of abbreviations see p. 4.]

is incomplete, as parethmoids do not meet at the mid-line. The olfactory nerve entered each nasal capsule through a posteromedial foramen in each parethmoid. From the base of the hammer-like palatine head a process extends anteriorly and then laterally, thus forming a notch in which the massive palatine malleolus is lodged. The laterally directed facet of this process is as long as the diameter of the articular facet of the palatine head but only one-third as wide. Endochondral parts of each parethmoid unite medially above the vomer.

Paired frontals roof the orbit. These bones meet the ethmoid anteriorly in a zigzag suture. Each frontal is limited posteriorly by the pterotic, sphenotic and conjoined parietals. Above the orbit, a broad shelf extends laterally from each frontal, contributing to support of the posterior supraorbital and dermosphenotic. An elongate groove incised in the frontal anterior to this broad shelf is occupied by a prong of the posterior suborbital. Farther forward a second groove receives the posterior nasal bone. Numerous small pits near the mid-line of each frontal indicate the position of sensory canal organs. In ventral view, above the orbit, the frontals show an elongate, shallow groove with a series of small foramina which carried superficial ophthalmic branches of the 7th nerve to the supraorbital sensory canal.

The sphenotic meets the frontal and pterotic dorsally, frontal and pterosphenoid on the rear wall of the orbit, and the prootic ventrally. An excavation in the lateral wall of the sphenotic forms the anterodorsal section of the hyomandibular fossa. The levator arcus palatini arises from a stout lateral process of the sphenotic. A foramen for the otic branch of the 7th nerve pierces the orbital face of this bone. This nerve emerged on the dorsal surface of the neurocranium through a foramen in the dorsoposterior side of the sphenotic.

Parietals fused at the mid-sagittal line completely separate the supraoccipital from frontals. This conclusion agrees with opinions of HAY (1898a) and STEWART (1900) and contrasts with that of CROOK (1892) and LOOMIS (1900). The latter two authors believed that the parietals were small and not joined mid-sagittally. Conjoined parietals are limited anterolaterally by frontals and laterally by pterotics. Posterolaterally each parietal produces the ventroanterior section of the parietoepiotic crest. The interdigitating parietoepiotic suture lies posterior to the level of the laterally directed sphenotic process. At the mid-line parietals form a ridge, which is a ventroanterior extension of the supraoccipital crest. An elongate, dense cluster of small knobs is developed along this ridge.

The supraoccipital is characterized by an enlarged crest with rounded anterior margin which is thicker than the bone behind it. The supraoccipital projects anteriorly below the parietals but does not reach the frontals. The anterior margin of the crest has a mean angle of 30 degrees (range 25-33 degrees in 14 specimens) to the horizontal body axis. This angle is less steep in smaller neurocrania.

The epiotic joins the parietal anteriorly, supraoccipital medially, pterotic laterally, and exoccipital posteroventrally. On the dorsal surface of the neurocranium the epiotic is characterized by a vertical ridge which attains approximately one-third the height of the supraoccipital crest. The posterodorsal end of the ridge is slightly swollen to provide an enlarged surface for attachment of epaxial muscles. A small accessory process projects posteriorly lateral to the main ridge. Epaxial muscles expanded onto the neurocranium between supraoccipital crest and epiotic crest. In posterior view (Fig. 7), a stout arm of the epiotic rises from the exoccipital. This arm forms the lateral wall of a pocket which is limited medially by the supraoccipital and floored by the exoccipital. This pocket is similar to the subepiotic fossa of *Sardinops* (PHILLIPS, 1942). The medial wall of the post-temporal fossa is formed by this vertical arm of the epiotic.

The pterotic covers most of the otic section of the neurocranial roof. This bone meets frontal and sphenotic anteriorly, parietal and epiotic mediodorsally, sphenotic, prootic, and exoccipital ventrally, whereas posteriorly the pterotic joins exoccipital and intercalar. The lateral temporal fossa is represented by a broad elongate depression on the dorsal surface of the pterotic. The middle section of the hyomandibular fossa is developed in the lateral surface of the pterotic. Below the hyomandibular fossa the pterotic forms the roof of the subtemporal fossa. In posterior view,

the post-temporal fossa extends anteriorly under the pterotic. This fossa, only 2-3 cm. in length, is limited anteriorly by convergence of epiotic and pterotic. A medially directed pterotic flange forms the floor of this fossa. A single foramen opens posteriorly from the medial wall of the pterotic. A sensory branch of the 7th nerve passed through this opening to the postotic sensory canal.

The parasphenoid is a stout, elongate bone divided anteriorly by the vomer. The parasphenoid does not meet the ethmoid. Below the orbit the parasphenoid is triangular in cross section with a gently curved ventral surface. Beneath the otic section of the neurocranium the parasphenoid lies approximately parallel to the horizontal body axis. The mean angle between otic and orbital sections of the parasphenoid is 160 degrees (range 158-170 degrees in 16 specimens). Below the posterior end of the prootic the parasphenoid is divided into two arms which terminate at the posterior end of the neurocranium. A short ascending process of the parasphenoid extends dorsally to form the lateral wall of the myodome canal. Two foramina penetrate the base of this flange. The anterior foramen carried the efferent pseudobranchial artery. The posterior foramen carried the internal carotid artery. A stout, elongate basipterygoid process extends ventrolaterally from the base of the parasphenoid just anterior to these foramina.

The prootic occupies more than half of the lateral wall of the neurocranium. Boundaries of this bone have been disputed by several authors. Hay (1898a) came closest to describing true limits of the prootic accurately. He summarized conclusions of earlier investigators but this bone and its foramina have never been described completely. On the posterior wall of the orbit the prootic joins pterosphenoid and sphenotic dorsally and basisphenoid medially. Medial wings of the prootic roof the anterior section of the myodome canal. On the lateral face of the neurocranium the prootic meets sphenotic and pterotic dorsally, exoccipital and basioccipital posteriorly, and parasphenoid ventrally. The ventroanterior section of the hyomandibular fossa is excavated in the prootic. Anterior and ventral walls of the subtemporal fossa are formed by the prootic. The prootic-exoccipital suture passes dorsomedially into the apex of the subtemporal fossa. A prong of bone arises from the prootic below this fossa and projects posterodorsally to join a similar, shorter prong from the intercalar (KU no. 991). The prootic bridge thus formed lies lateral to the junction of exoccipital, basioccipital, and prootic. Two ridges diverging posteroventrally are developed on the prootic below the subtemporal fossa. Levator muscles of the branchial arches arose from the prootic between these ridges. There is no external evidence of prootic or pterotic osseous capsules of the semicircular canals.

Two foramina appear on the lateral face of the prootic. The upper foramen is larger and lies just below the prootic section of the hyomandibular fossa. The hyomandibular branch of the 7th nerve passed through this foramen. The lower foramen is smaller and opens ventroposteriorly from the base of the posterior of the two ridges described above. This foramen leads into a prootic canal which passes anterodorsally through this ridge into the trigeminofacial

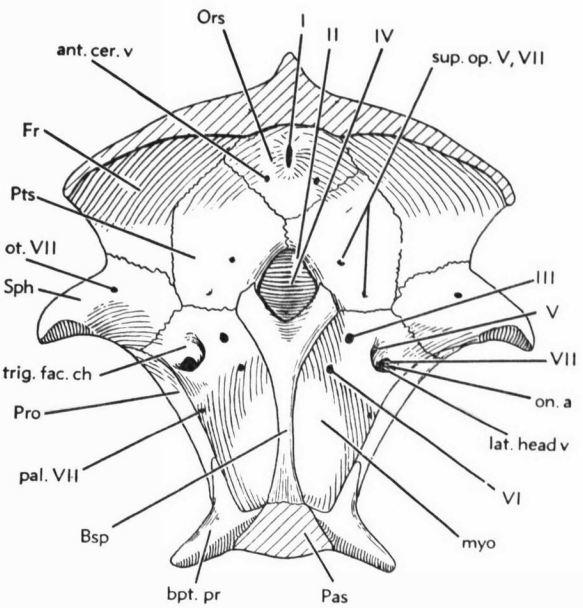


FIGURE 8. *Xiphactinus audax* LEIDY. Restoration of postorbital neurocranial wall. Based on KU No. 738, ×0.5. [For explanation of abbreviations see p. 4.]

chamber. On KU no. 9888 a second foramen opens posteriorly from this canal just dorsal to the main opening. On the basis of comparison with *Chirocentrus*, clupeids, *Notelops*, and *Salmo* (GOODRICH, 1930), I believe that the posterior palatine branch of the 7th nerve, as well as the orbitonasal artery, passed through this foramen. This artery may have entered the prootic canal separately when two foramina were present, as on KU no. 9888.

The lateral head vein canal lies just medial to the ventrolateral lip of the subtemporal fossa. The posterior foramen of this canal opens about 1 cm. in front of the origin of the prootic bridge. The canal passes anteriorly through the prootic and emerges from the trigeminofacial chamber on posterior wall of the orbit.

The posterior orbital wall is best exhibited by KU no. 733 (Fig. 8). The trigeminofacial chamber lies entirely within the prootic and includes two foramina, a larger lateral foramen and a smaller, medial, more dorsally situated foramen. Mandibulo-maxillary branches of the 5th nerve entered the orbit through the medial opening, while buccal and otic branches of the 7th nerve, lateral head vein, and orbitonasal artery traversed the lateral opening. A small foramen medial to the trigeminofacial chamber carried the oculomotor nerve. A pair of foramina open into the myodome canal through each medial wing of the prootic. The smaller, lateral foramen carried the palatine branch of the 7th nerve. The larger, medial foramen brought the 6th nerve into the myodome canal.

The pterosphenoid joins the basisphenoid posteromedially, prootic posteriorly, sphenotic posterolaterally, frontal anterolaterally, and orbitosphenoid anteriorly. Just posterior to the orbitosphenoid, the paired pterosphenoids

meet at the mid-sagittal line anterior to the optic foramen. The pterosphenoid and basisphenoid enclose the optic fenestra. Two small foramina open dorsally from the pterosphenoid near the juncture of this bone and the prootic. These foramina carried secondary branches of the 5th and 7th superficial opthalmic nerves. The 4th nerve probably emerged through the optic foramen along with the optic nerve, because no foramen for the 4th nerve is developed in the pterosphenoid.

The single orbitosphenoid extends anteriorly from pterosphenoids and joins the frontals laterally. There is no bony connection between orbitosphenoid and parethmoids. Olfactory nerves lay dorsal to the orbitosphenoid and entered the orbit through a medial opening midway along the length of this bone. A posterolateral foramen for the anterior cerebral vein penetrates the orbitosphenoid.

The basisphenoid has a stout anteroposteriorly expanded ventral process which divides the myodome canal. This process is anchored firmly to the parasphenoid. Dorsolateral wings of the basisphenoid limit the anterior opening of the endocranial cavity and separate optic fenestra from the infundibular foramen. The latter is enclosed by basisphenoid and prootic.

The basioccipital forms the posteroventral corner of the neurocranium. Half a centrum is fused to the basioccipital. The lateral surface of the basioccipital is concave and a branch of the swim bladder extended onto the neurocranium along this concavity.

The exoccipital joins the prootic anteriorly, basioccipital ventrally, and prootic dorsally. Much of the lateral face of the exoccipital is covered by the intercalar. In posterior view (Fig. 7) the paired exoccipitals meet above the foramen magnum and support the base of the supraoccipital. Slender wings arising from that part of the exoccipital which surround the foramen magnum project posteriorly. Posterior facets of these wings are flattened and articulate with the neural arch of the first centrum. The floor of the subepiotic fossa is formed by the exoccipital. A depression approximately 0.5 cm. in diameter lies lateral to the foramen magnum. This depression with irregularly crenulated edges marks the point at which intermuscular bones termed osseous brushes (Ridewood, 1904a) were attached to the neurocranium. These bones which extend posteriorly within the epaxial musculature, are seen on FH no. 5026 and DNHM no. 1667. Dorsomedial to the depression lodging these intermuscular bones lies a foramen for an occipital nerve. A large canal approximately 1 cm. in diameter runs anteroposteriorly through the exoccipital into the subtemporal fossa. A foramen from a second canal enters the posteromedial face of the main canal. The second canal angles anteromedially into the endocranial cavity (AMNH no. 7347, KU no. 477) and carried the 10th nerve. The lateral head vein travelled through the main canal lateral to the 10th nerve. Branchial branches of the 9th nerve emerged from the glossopharyngeal foramen just in front of the foramen for the 10th nerve and passed posteriorly through the main canal with the 10th nerve. The supratemporal branch of the 9th nerve extended dorsally from the glossopharyngeal foramen along a groove on the posterodorsal surface of the subtemporal fossa. This branch then penetrated the exoccipital and emerged lateral to insertion of the osseous brushes.

The intercalar forms the dorsolateral corner of the neurocranium. This bone joins the pterotic dorsally in a zigzag suture and the exoccipital limits the intercalar medially and ventrally. The prootic bridge abuts on an anterolateral projection of the intercalar. Hay (1898a) suggested that a wing from the intercalar projected ventrally over the basioccipital as in *Tarpon*. The ventral border of the intercalar is intact on several specimens of *Xiphactinus audax* and there is no suggestion of a missing wing (KU nos. 165, 168). A round protuberance on the posterior face of the intercalar characterized by spikes radiating from its center, receives the ventral arm of the posttemporal via a ligamentous connection. The posterior section of the hyomandibular fossa is excavated in the intercalar.

A pair of well-ossified sclerotic bones ring each eyeball. Fragments of a posterior osseous cup appear on KU no. 735. The cup is better preserved on specimens of *Ichthyodectes*.

[*Maxillary-mandibular bones.*] The upper jaw, formed by the premaxillary and maxillary, moves as a unit. The maxillary extends anteromedial to the premaxillary, which is firmly joined to the maxillary by an arrangement of short ridges and grooves arising from the medial surface of the premaxillary and interdigitating with similar ridges and grooves on the maxillary.

Premaxillary profile is oval except for a straight dental border (Fig. 9). Dorsally and posteriorly this bone is thin, with scalloped edges, whereas the anterior margin is broad and flat. Ligaments connecting premaxillary and ethmoid were attached to a flat facet on the dorsomedial surface of each premaxillary. Anterior borders of the premaxillaries were joined to each other by ligaments.

Premaxillary teeth are lodged in sockets which extend as far or farther into the bone than the crown protrudes beyond the alveolar border. Alveoli (2-5) are present in each premaxillary (mean 2.6 for 110 specimens; standard deviation 0.8). In general two teeth are present. These project ventroanteriorly and are unequal in size. One may reach 6 cm. in crown height while the other is just developing beyond the alveolar border. Of 42 premaxillaries with two or more alveoli the first alveolus shows a tooth in 69 percent of the specimens and the second alveolus in 62 percent. Twenty-six of the 42 premaxillaries have a third alveolus which exhibits a tooth in 73 percent of the specimens. Eleven premaxillaries with a fourth alveolus show a tooth in 73 percent of the specimens. Two premaxillaries have a fifth alveolus but this is not occupied by a tooth in either. The number of alveoli, as well as sequence of alveoli with and alveoli without teeth, can vary between right and left premaxillaries of the same individual. Of 15 specimens with right and left premaxillaries of the same individual, 3 pairs differ by one alveolus. Only 4 of them show the same pattern of alveoli with and without teeth on each pair of premaxillaries.

Mean ratio of alveolar border length to diagonal height is 39 for premaxillaries with 2 alveoli (range 32-53 in 50

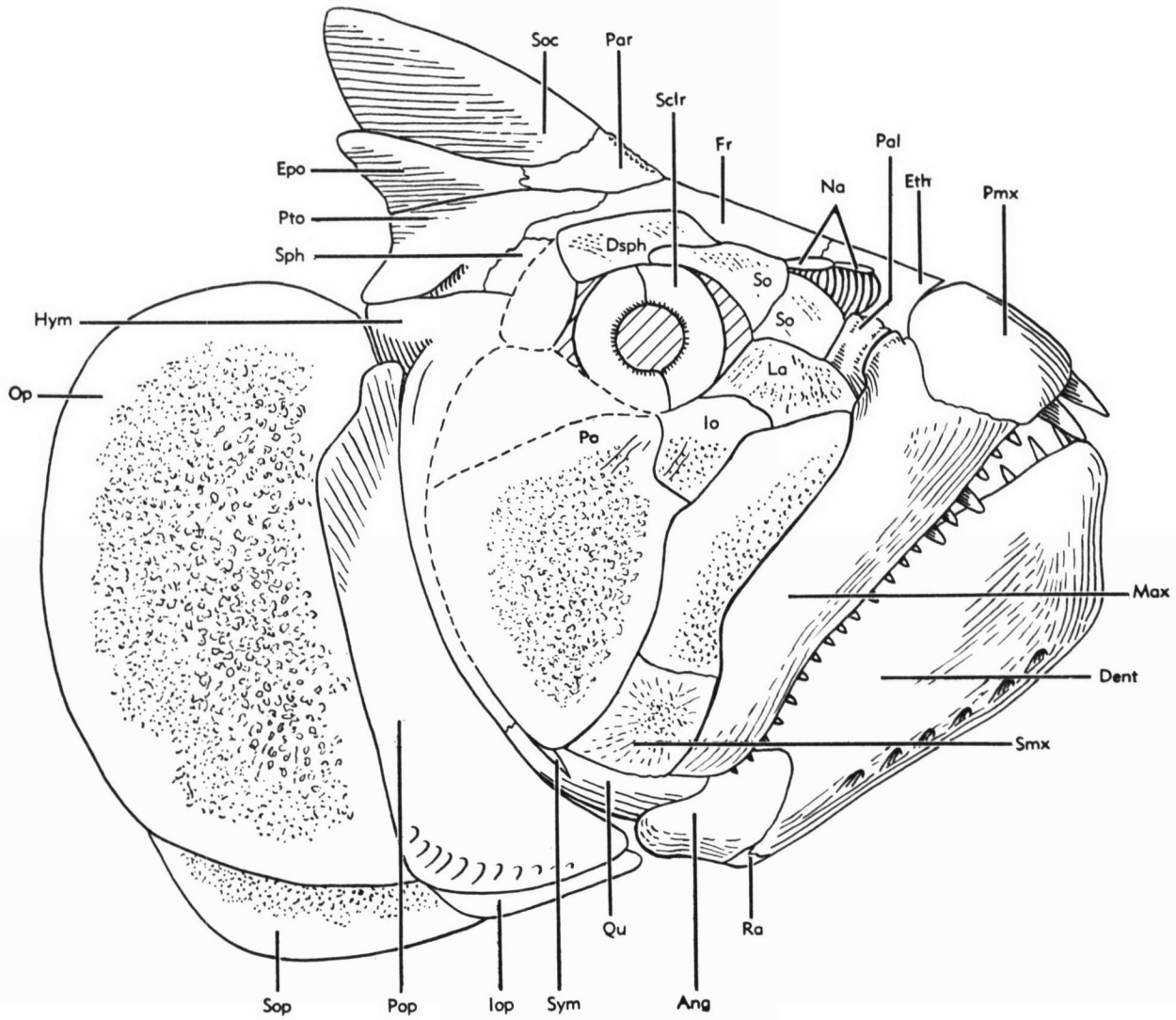


FIGURE 9. *Xiphactinus audax* LEIDY. Restoration of head. Based on KU No. 320 and No. 103, ×0.3. [For explanation of abbreviations see p. 4.]

specimens); 48 for premaxillaries with 3 alveoli (range 37-60 in 28 specimens); and 54 for premaxillaries with 4 alveoli (range 50-58 in 11 specimens). Mean length of the premaxillary alveolar border is 4.1 cm. (range 2.7-6.2 cm. in 91 specimens; standard deviation 1.8 cm.).

The maxillary is a heavy elongate bone. The anterodorsal end meets the ethmoid and the posterior end lies below the rear of the orbit. Medial to the premaxillary the maxillary is less than half as thick as posterior to the premaxillary. Two condylar surfaces characterize the dorsoanterior surface of the maxillary. An anterior condyle developed on dorsal and medial surfaces abuts on a facet formed by vomer and ethmoid. The posterior and larger condyle lies behind that part of the maxillary which is covered by the premaxillary. This flat condyle articulates with the palatine malleolus. STEWART (1900, pl. 41) figured condyles of 14 specimens to demonstrate their variation in outline from individual to individual. He also illustrated maxillaries of 12 individuals to show profile variation of this bone (STEWART, pl. 37-40). Behind the posterior condyle the maxillary profile drops abruptly and continues posteriorly in a straight line. The dorsolateral margin of this section bears an elongate groove in which circumorbitals are inserted anteriorly and supramaxillaries posteriorly. In dorsal view the maxillary tapers posteriorly. The ventral border is essentially straight. The medial surface is smooth, but several longitudinal ridges and grooves are developed on the lateral surface. Two supramaxillaries are present. The anterior is rectangular; the posterior roughly square-shaped.

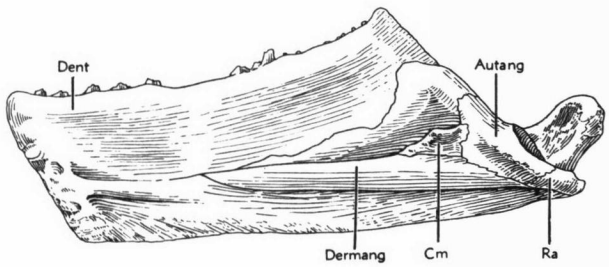


FIGURE 10. *Xiphactinus audax* LEIDY. Internal view of mandible. KU No. 116, ×0.25. [For explanation of abbreviations see p. 4.]

Mean maxillary length measured along the alveolar border from juncture with premaxillary to most posterior alveolus is 20.5 cm. (range 14.5-28 cm. in 52 specimens; standard deviation 3.6 cm.). Mean height of the maxillary at the posterior condyle is 9 cm. (range 5.5-13 cm. in 81 specimens; standard deviation 1.6 cm.). Mean ratio of maxillary height to length is 43 (range 35-53 in 50 specimens).

Maxillary teeth are conical and like those of the premaxillary, the surface is smooth. Teeth are generally present in alternate alveoli, although several jaws show two or more adjacent alveoli occupied by teeth. In such specimens crown height of the teeth varies because they belong to alternate replacement series. The mode of tooth replacement in *Xiphactinus* has been described by LOOMIS (1900) who showed that a young tooth appears on the medial wall of an old tooth just below the alveolar border. As the young tooth develops, roots and cement of the old tooth are absorbed. When a replacement tooth nearly fills an alveolus, the crown of the old tooth breaks off and the new tooth is cemented to the walls of the alveolus. Sectioned jaws which I have examined confirm LOOMIS' findings. LOOMIS also described the order of tooth replacement. The sequence begins at the rear of the dentition with small, young teeth not filling an alveolus and proceeds anteriorly with progressively larger teeth occupying alternate alveoli until a fully erupted tooth fills an alveolus. From the small tooth to the fully erupted one this sequence involves approximately 4 stages, each separated from the next by an alveolus which is part of another replacement series.

Mean number of maxillary alveoli is 32.6 (range 22-39 for 31 specimens; standard deviation 4.4). In most specimens dimensions of teeth must be determined by study of alveolar size and shape because crowns of the teeth are not preserved. The first 1-5 teeth behind the premaxillary gradually increase in width, the largest attaining less than 0.5 cm. in diameter at the alveolus. These teeth are followed by 3-5 larger ones approximately 1 cm. in diameter, lying below and posterior to the level of the palatine condyle. The teeth which occupy a tumescent region of the alveolar border may reach 4 cm. in crown height. Alveoli posterior to the large teeth are approximately 0.5 cm. in diameter and the teeth in them may reach 1 cm. in crown height. The more posterior of the alveoli rapidly diminish in diameter. The wide range in number of maxillary alveoli arises from variation in number of the posterior alveoli. The number of maxillary alveoli can vary between left and right sides of the same individual. Thus, the left maxillary of KU no. 168 has 30 alveoli and the right maxillary 26; NMC no. 8799 has 36 right and 30 left, but AMNH no. 1680 exhibits 31 alveoli in each maxillary.

Four bones comprise the mandible (Fig. 10). The dentary is its major element. At the symphysis this bone is characterized by irregular grooves and ridges from which ligaments arose to unite left and right mandibles. In profile the dentary alveolar border curves gently or in some specimens steeply (NMC no. 8151) downward along the anterior one-third of the dental border before gradually rising to the coronoid process. Organs of the mandibular sensory canal are lodged in a series of six pits on the ventrolateral surface of the dentary. Profiles of 12 mandibles were figured by STEWART (1900, pl. 34, 35, 37-40, 45B, 48). Mean length of the symphysis is 8.7 cm. (range 6.0-13.5 cm. in 81 specimens; standard deviation 1.6 cm.). The anterior margin of the dentary bears a mean angle of 123 degrees to the ventral border of the dentary (range 117-130 degrees in 42 specimens; standard deviation 3.3 degrees).

The angular includes dermal and endochondral divisions, of which the dermal component is the larger. The lateral wall of the mandible ventral and posterior to the coronoid process is formed by the dermangular, a process of which projects anteriorly medial to the dentary. Part of the process forms an elongate flat plate at approximately 90 degrees to the dentary. The intramandibular section of the adductor mandibulae is inserted on the dermangular plate and the dentary. An expanded process of the dermangular projects dorsoposteriorly behind the mandibulo-quadrate articulation, the posterolateral part of which is formed by the dermangular, the autangular comprising the major element of this socket. The autangular, confined to the medial surface of the dentary, meets the dermangular in a zigzag suture in front of the mandibulo-quadrate articulation.

A separate retroarticular caps the posteroventral end of the mandible. A short, compact bone of irregular dimensions lies on the medial surface of the mandible anterodorsal to the juncture of autangular and dermangular. This bone, first described by STEWART (1900), is the coronomeckelian. Its dorsal facet received part of the adductor mandibulae.

Measured from the anteroventral end of the dentary to the posterior end of the dermangular, mean mandibular length is 29.5 cm. (range 20-40.5 cm. in 41 specimens; standard deviation 5.3 cm.). Mean height of the coronoid process from the base of the mandible is 12.3 cm. (range 8.4-16 cm. in 20 specimens; standard deviation 1.6 cm.). Mean length of the alveolar border is 21.3 cm. (range 16.5-25.5 cm. in 32 specimens; standard deviation 2.4 cm.).

Variation in size and arrangement of the mandibular alveoli was demonstrated by STEWART (1900). Mean number of mandibular alveoli is 21.7 (range 16-25 in 26 specimens; standard deviation 2.1). Two large alveoli (approximately 1.5 cm. long, 1 cm. wide) at the anterior end of the dentary are followed by a diastem or one to several

small alveoli (less than 0.5 cm. in diameter). These are succeeded by 2-4 alveoli approximately 1.5 cm. long and 1 cm. wide. Posterior alveoli are of equal size (approximately 1 cm. in diameter) except for the last 2 or 3 which measure 0.5 cm. in diameter. Proportions of dentary alveoli from anterior to posterior end of the alveolar border are less consistent from one individual to another than are proportions of maxillary alveoli. Anterior mandibular teeth may reach 7 cm. in crown height; posterior teeth are approximately 1-2 cm. high.

[*Hyopalatine bones.*] The five hyopalatine bones unite the neurocranium and jaws flexibly but firmly (Fig. 11). The largest bone, the hyomandibular, curves slightly forward from its articulation with the neurocranium and ends ventrally medial to the quadrate. The neurocranial head of the hyomandibular presents an elongate dumbbell appearance in dorsal view. The opercular head is dorsoventrally elongate. A short, vertical crest appears on the medial surface of the hyomandibular at the level of the opercular head. Anterior to this crest is a large triangular depression penetrated by a foramen for the hyomandibular branch of the 7th nerve. The adductor hyomandibulae inserted in this depression. On the lateral face of the hyomandibular a dorsoventral ridge extends nearly the entire length of the bone. The preoperculum fits against the posterior face of this ridge. At the level of the opercular head, the ridge curves anteriorly and passes into the general surface of the hyomandibular. Two oval depressions, one above the other, occur on the lateral surface of the hyomandibular in front of the opercular head and behind the dorsoventral ridge. Ventral slips of the dilatator operculi arose from these depressions. A large concavity of irregular outline lies anterior to the dorsoventral ridge. The foramen for the hyomandibular branch of the 7th nerve opens into this depression. A short wing of bone triangular in profile projects from the anterior margin of the hyomandibular just below the neurocranial head. As in *Clupea* (Kirchhoff, 1958), part of the levator arcus palatini was inserted on this process. The hyomandibular overlaps the metapterygoid anterolaterally in such manner that the hyomandibular just meets the mesopterygoid.

The metapterygoid comprises half of the palatal roof. This bone joins the quadrate ventrally, hyomandibular posteriorly and dorsally, mesopterygoid anteriorly, and ectopterygoid anterolaterally. The longitudinally arched mesopterygoid meets the palatine anteriorly and metapterygoid posteriorly. The medial border of the horizontal section of the mesopterygoid is curved slightly so that a narrow elongate opening is left between parasphenoid and metapterygoid. The ventrolateral section of the mesopterygoid joins the ectopterygoid. Along the dorsal border of the hyopalatine arch the mesopterygoid and metapterygoid form a transverse groove which is directed slightly forward. The groove receives the basipterygoid process. Small, fragmentary patches of chondrified cartilage on medial surfaces of the mesopterygoid and ectopterygoid contain fine palatal teeth. Tubercles of irregular outline seen on the meta- and mesopterygoid (Stewart, 1900, pl. 42, fig. 4) are impressions produced by compression during fossilization of thin palatal bones against the short gill rakers and pieces of palatal dentiton.

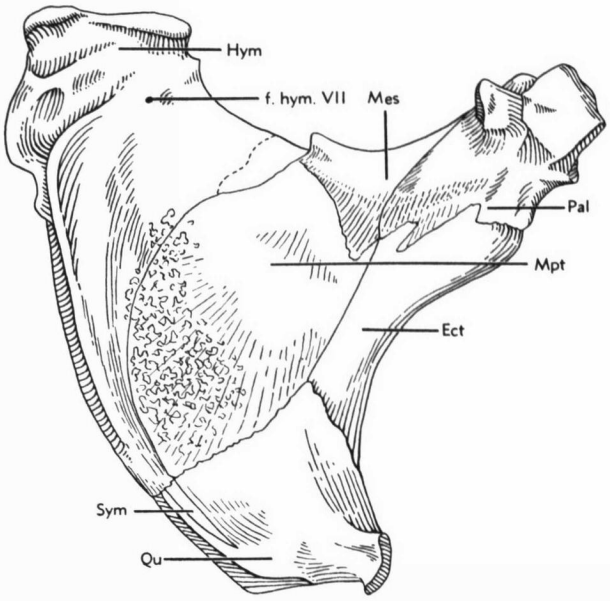


Figure 11. *Xiphactinus audax* Leidy. External view of hyopalatine bones. KU No. 168, ×0.3. [For explanation of abbreviations see p. 4.]

The elongate, boomerang-shaped ectopterygoid resembles that of other isospondyls. The ectopterygoid meets the quadrate posteriorly, meta- and mesopterygoid dorsally, and joins the palatine anteriorly. The palatine overlaps the ectopterygoid posteroventrally and meets the mesopterygoid posteriorly. The palatine is characterized anteriorly by a swollen malleolus which abuts on the parethmoid dorsally and maxillary ventrally. Mean ratio of palatine malleolar height to length is .84. Outline of dorsal and ventral facets of the palatine malleolus varies from individual to individual.

The quadrate is triangular in outline. The apex, directed ventrally, is bent forward and ends in a rounded condyle which articulates with the mandible. A dorsoventral groove on the posterolateral face of the quadrate marks the juncture of preoperculum and quadrate. The spikelike symplectic lies in an elongate slot cut into posterodorsal section of the quadrate. Relationships of hyopalatine bones may best be seen on AMNH no. 7321 and KU nos. 124, 477.

[*Circumorbital bones.*] These bones are fragile and no specimen exhibits a complete set (Fig. 9). Two large, platelike supraorbitals cover the orbit anterodorsally. The posterior supraorbital has a stout prong which tapers anteroventrally and lies along the posterior border of the parethmoid. The smaller, squarish anterior supraorbital covers the parethmoid.

The lacrimal is a short, deep bone. It is followed by the short, trapezoidal infraorbital. The first postorbital is elongate and extends posteriorly to the preoperculum. At

least one, and perhaps two additional postorbitals lie above the first postorbital but only fragments of these bones are preserved. The dermosphenotic is an enlarged, centrally thickened, rectangular bone in contact with posterior supraorbital anteriorly and dorsalmost postorbital ventrally. Branches of the infraorbital sensory canal can be traced on suborbital bones. Two nasal bones are present on each side (Fig. 9). The posterior end of the longer, wider, rod-shaped posterior nasal is inserted in a groove on the lateral surface of the frontal and projects over the posterior part of the nasal capsule. The narrower, flatter, anterior nasal lies above the anterodorsal region of this capsule.

[*Opercular bones.*] The preoperculum is elongate dorsoventrally (Fig. 9) and expanded as a broad plate ventrally. The anterior border is thickened. A row of 10-13 pits for sense organs of the preopercular sensory canal open ventrally or ventroposteriorly from the ventrolateral surface of the preoperculum. The posterior 6 of these pits lead into grooves which gently curve posteriorly.

The operculum, 1.25 times higher than long, resembles a letter "D" facing posteriorly. An elongate cup for the opercular head of the hyomandibular lies just below the dorsal opercular margin. Irregularly arranged tubercles embossed on several opercular are produced by compression against the gill rakers.

Suboperculum and interoperculum were described by McClung (1908). The suboperculum (Stewart, 1900, pl. 45, fig. 3, KU no. 168), approximately as long as the operculum, is rectangular in outline and thickened along the mid-longitudinal line. A dorsoanterior process of this bone extended under the operculum. McClung described a depression of irregular outline on the anterolateral surface of the suboperculum. This area was covered by the interoperculum. Tubercles on the lateral face of the suboperculum, as on the operculum, result from compression against gill rakers.

The interopercular described by McClung (1908, see Stewart, 1900, pl. 44, fig. 1, 5, left and right sides, described as "bones of uncertain position," KU no. 168) are incomplete. The anterior face of each interoperculum shows a roughened facet. Ligaments arising from this facet ran to posterior end of the mandible. A longitudinally thickened wing of bone extends posteriorly from this facet.

[*Hyobranchial bones.*] Several ceratohyals are preserved (Stewart, 1900, pl. 42, fig. 7, KU no. 168). These elongate slender bones show a dorsoventrally deepened concave depression posteriorly. A dorsal and ventral facet on the anterolateral side of each ceratohyal articulates with the hypohyals. Least width of the ceratohyal, posterior to hypohyal articulation, is contained 4 times in longitudinal length of ceratohyal. Bones of the branchial arches are well-ossified longitudinally grooved rods. Gill rakers include sigmoid-shaped (KU no. 731), distally blunt processes about 1 cm. long and 0.5 cm. thick. These structures alternate with slightly longer, thinner, spikelike rakers.

[*Sensory canals.*] Except for a few pits on the anteromedial surface of each frontal, dorsal sensory canals have lost contact with dermal bones and lie above the epaxial musculature. Locations of preopercular, mandibular, and infraorbital canals have been noted in description of the bones which they traverse.

[*Vertebrae and ribs.*] In natural position the vertebral column forms a straight line. The number of vertebrae ranges from 85-89 (mean 86.2 in 9 specimens) with 52-57 abdominal (mean 53.4 in 9 specimens) and 29-33 caudal (mean 31.9 in 8 specimens).

The first centrum (KU nos. 168, 735) is slightly more than 2 cm. in length and approximately 5 cm. in height and width. Succeeding centra increase in length and by the 8th or 9th are 3-4 cm. long and 5-6 cm. in height and width. In transverse view most centra appear circular but the dorsal surface of anterior 3 or 4 centra is slightly flattened. All are deeply biconcave except the first, which has a flat anterior surface and is deeply concave posteriorly. Each centrum, except the first, is perforated by a small notochordal canal. In transverse section (KU nos. 166, 929) a ring of dense bone occupies the central part of each centrum. The cancellous outer area is characterized by a thin irregularly interlaced network of bone extending outward from the dense center.

The shape of ridges and depressions on the centra is characteristic of *Xiphactinus*. A broad, longitudinal lateral ridge between two longitudinal grooves first appears on the fourth centrum but is not well developed until the 7th or 8th centrum. Dorsoventral height of this ridge at the middle of a centrum is approximately twice the width of the groove opening above or below the ridge, which diminishes in height on the posterior caudal centra and disappears by the 6th from last centrum. Working with incomplete or crushed vertebral columns, Stewart (1900) decided that presence or absence of ridges and grooves varied from individual to individual. Examination of intact, uncrushed specimens shows that longitudinal ridge and grooves are present on all centra within the limits stated above. A pair of dorsal depressions appear on all centra. Anteriorly these depressions are rounded pits, but posteriorly they increase in length and by the 9th or 10th centrum are elongate cavities. Bases of the neural arches insert in these hollows. Depressions for hemal arches first appear on mid-abdominal centra and characterize all subsequent centra.

The caudal skeleton comprises 6 vertebrae but only the last 4 are turned slightly upward. Stewart noted that a small prong of bone projected posterodorsally from the last centrum on KU no. 168. The piece of bone, probably a uroneural, is now missing. It was not fused to the last centrum for there is no evidence of a break at the posterior end of the centrum. Hemal spines of caudal centra 25, 26, 27 and 28 (FH no. 5026) are broad-based and swollen. The first spikelike hypural is fused to the terminal centrum and bears a hemal canal. A small process projects posteriorly from the base of the hypural just below its juncture with the centrum. The 2nd hypural is attached to the post-terminal centrum (Gosline, 1960) by a rounded head. The hypural is spatulate distally. A notch in the distal border above a posteroventrally projecting process characterizes the hypural. The 3rd hypural shown on the caudal skeleton figured by Stewart (1900, pl. 47B, fig. 1)

is the 2nd of another individual. According to COPE (1875, pl. 44, fig. 2) the 3rd hypural is rectangular and lacks a distal notch and process. This agrees with the statement of GOSLINE that in most lower teleosts the 3rd hypural is a narrow strut not expanded posteriorly. It is a rod-shaped bone (KU no. 103). Four additional short, rectangular hypurals are present on the figure given by COPE. Structure of the dorsal caudal skeleton cannot be determined from available material.

The neural arches of anterior abdominal centra articulate with those in front and behind. A process extends posteriorly from the base of each neural arch. A rounded medial facet on the process articulates with a shallow cup-like facet on the anterior end of the next posterior neural arch (HAY, 1898a, fig. 15, 16). Such articulations occur from the first to 42nd vertebrae of FH no. 5026. Bases of neural arches posterior to the 42nd are triangular and not connected to posterior neural arches and these are not fused to the centra. Neural spines extend dorsoposteriorly nearly to the dorsal body line. Anterior neural spines are broader than posterior ones. The first few caudal neural spines curve gradually, whereas posterior ones bend sharply caudally. Interneural bones appear on OUSM no. 1-0-S72, AMNH no. 8443, and CM no. 4101 between each neural spine from the back of the neurocranium to base of the dorsal fin.

Hemal arches are co-ossified but not fused to the centra. Hemal spines curve posteriorly but not, initially, as sharply as neural spines. HAY (1898a, fig. 12-14) described and illustrated neural and hemal arches in an inverted position (corrected, HAY, 1903a). Hemal arches arise on the 31st centrum of AMNH no. 8443 and FH no. 5026; on 32nd of DNHM no. 1667 and 33rd centrum of CM no. 4101.

Three series of ribs are present. Epipleural ribs inserted in teardrop-shaped depressions in the anterior part of the lateral ridge of each centrum. The depressions appear on the 5th to 40th centra of KU no. 168 and the 5th to 38th of FH no. 5026. Anterior to the 5th centrum epipleural ribs were attached near the base of each neural arch.

Epineural ribs arise from bases of the first 42 neural arches (DNHM no. 1667, FH no. 5026). Epineural ribs of the first two dozen centra project posteriorly in a nearly straight line for the length of 10 vertebrae before curving sharply upward. Posterior epineurals are shorter and rise almost vertically behind each neural spine.

The first pleural rib arises close to the ventral border of the 2nd centrum. The point on the centrum to which this rib is attached rises so that the pleural ribs of the 4th centrum originates from the lower of the 2 longitudinal grooves of each centrum. Except for 2nd and 3rd centra a parapophysis is present on each centrum which bears a pleural rib. Each parapophysis consists of a flat plate inserted into the ventral groove of a centrum and a short distally rounded process extending laterally to receive the rib. Heads of the 7th to 20th pleural ribs splay out over parapophyses and ventrolateral surface of the centra. Within 5 centra from origin of the hemal arches, pleural ribs become attached to the arches and parapophyses disappear.

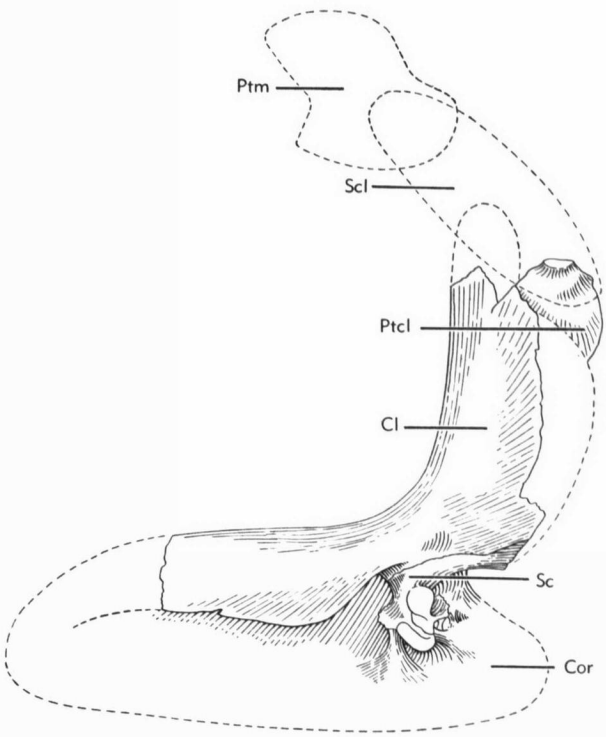


FIGURE 12. *Xiphactinus audax* LEIDY. Restoration of pectoral girdle. KU No. 183, ×0.2. [For explanation of abbreviations see p. 4.]

[*Pectoral and pelvic girdles.*] Seven bones comprise the pectoral girdle (Fig. 12). The post-temporal (CM no. 4101, Oakley Public School no. 13-25, NMC no. 8152) is a flat bone, quadrilateral in outline and approximately 15 cm. in maximum height. A broad, thin wing of the post-temporal projects anteriorly toward the epiotic. The wing is not as high as the supraoccipital crest. Another wing extends over the posterolateral margin of the neurocranium. A longitudinal, medial ridge arising near the posterior border of the post-temporal is prolonged anteriorly as a stout process. The process was attached to the intercalar by a stout ligament. HAY (1898a) erroneously described the post-temporal of *Xiphactinus* as short, thick, and less than 2 cm. in length. He probably confused a fragment of an expanded anterior neural spine with the post-temporal. There is no evidence of an extrascapular.

A complete supracleithrum separated from post-temporal and cleithrum is not preserved. But because other parts of the *Xiphactinus* and *Ichthyodectes* pectoral girdles are similar, we may conclude that form and position of the supracleithrum is similar in both genera. [See description of the *Ichthyodectes* supracleithrum.]

MCCLUNG described and illustrated (1908, fig. 6) a bone which he identified as a supracleithrum (KU no. 165). He also referred to the supracleithrum one of the bones which STEWART (1900, pl. 44, fig. 2, KU no. 168) described as of "uncertain position." These supposed su-

pracleithra are actually dorsal postcleithra (Fig. 12). The post-cleithrum lies medial to the cleithrum, rather than lateral to it, as does a supracleithrum. Also, postcleithrum and post-temporal are not connected. The postcleithrum is thickened anteriorly and sutured to a posteromedial prominence on the cleithrum. A 2nd postcleithrum may be represented by another of the bones described by STEWART (1900, pl. 44, fig. 3, KU no. 168) as of "uncertain position." One side of this bone is hollowed out and the other side bears a rounded elongate ridge. It is possible, however, that this is a post-temporal fragment.

The cleithrum is shaped like a boomerang, with vertical and horizontal arms of equal length. The vertical arm is expanded anteroposteriorly as a broad wing. The lateral surface of the vertical arm is marked with deeply incised striae, which run dorsally and dorsoposteriorly from the base of the arm. The horizontal arm is divided into medial and lateral plates. The coracoid is attached to the medial plate. The lateral plate extends ventrolateral to the coracoid.

The coracoid joins the medial plate of the cleithrum dorsally, and the mesocoracoid and scapula posterodorsally; ventrally the paired coracoids meet to form a keel at the mid-ventral line. In posterior view, each coracoid shows a hemispherical pocket medial to a similarly shaped pocket incised in the scapular and coracoid. The 3rd pectoral actinost was inserted in the coracoid pocket. A stout ridge rises from the posterolateral surface of the coracoid to join the scapula ventral to the lowest scapular condyle. A foramen runs anteroposteriorly between this ridge and the thin coracoid plate. The foramen may be divided (KU no. 243) by several bars passing from ridge to plate or be a single opening (KU no. 246).

The scapula meets the cleithrum and mesocoracoid dorsally and the coracoid ventrally. A broad process of the scapula extends dorsally medial and posterior to the cleithrum. The process is limited anteriorly by the mesocoracoid. The stout condylar section of the scapula projects laterally to the vertical body axis at an angle of approximately 45 degrees. Three articular facets characterize the condylar surface. The uppermost, anteroposteriorly convex facet is the largest and articulates with the first ray of the pectoral fin. The middle facet varies in shape. It may be flat (KU no. 174) or concave (KU no. 183, 246), twice as high as wide (KU no. 183) or about equal in length and width (KU no. 160). The lowest facet is almost flat (KU no. 246) or slightly concave (KU no. 160). Its ellipsoid outline is oriented in an anteroposterior direction (KU nos. 233, 246) or tilted at an angle to the horizontal axis of the body. A posterior facing hemispherical pocket excavated in scapula and coracoid receives the 2nd pectoral actinost. The suture between coracoid and scapula runs diagonally across this pocket.

The mesocoracoid is a stout vertical strut sutured ventrally to scapula and coracoid and extending dorsally medial to the cleithrum. The dorsal end of the mesocoracoid passes smoothly into the cleithrum below attachment of cleithrum and postcleithrum. A large anteroposterior canal is limited laterally by the scapula and medially by the mesocoracoid.

There are at least 3 proximal pectoral actinosts. The first (KU no. 167) is a flat bone which resembles the navicular of *Equus*. Two anteroposteriorly elongate, elliptical, concave facets are developed on the proximal surface of this bone. The upper facet is smaller than the lower one and articulates with the middle of 3 scapular facets. The lower, olivoid facet articulates with the lowest of the 3 facets. Two smaller, round, flat-surfaced facets on the distal side of the actinost articulate with distal actinosts, if such were present, or directly with the 2nd pectoral fin ray. The 2nd and 3rd actinosts are T-shaped. The round head at the base of the vertical bar of the 2nd actinost is inserted into the pocket formed between scapula and coracoid. The vertical bar was also anchored by ligaments to a depression on the distal surface of the first actinost. The head of the 3rd actinost is inserted in the hemispherical pocket lying entirely within the coracoid. Distal actinosts were probably present but only one pair of such bones can be identified. Among the material of CMNH no. 10421 are a pair of elongate, rounded bones. One end of each is gently rounded; the other has a curved articular facet. Just beyond the facet a foramen passes through the bone. These bones resemble the first distal actinost of *Chirocentrus*.

The pelvic girdle was adequately described and illustrated by HAY (1898a, figs. 10, 11). The longest basipterygium (FH no. 5026) measures 21 cm. The basipterygia of each side meet at the mid-sagittal line in a robust, interdigitating suture. Pelvic bones reach their greatest height posteriorly, at the site of facets for articulation of the pelvic fin. A thin, laterally broadened arm extends forward from the articulation of each pelvic fin. The lateral border of the arm is expanded dorsoventrally. A medial, lower, dorsoventral expansion of the transversely broadened arm extends anteriorly from the base of the facet for the first pelvic fin ray, gradually passing into the anterior pronglike extension of the transversely broadened arm. Basipterygial articular facets consist of a flat, circular or ellipsoidal disc dorsally and a flat, elongate ellipse ventrally. The lower facet is twice the size of the upper. The facets lie approximately one above the other and receive the first pelvic fin ray. A short, posterolaterally directed, rounded protuberance lies between the two facets. Medial to the protuberance is a 2nd one directly posteriorly. Pelvic actinosts are not preserved but small, flattened disc-shaped bones must have participated in articulation of all pelvic fin rays except the first.

[*Fins.*] The Fort Hays specimen (FH no. 5026) is especially valuable for information on fin position and fin ray counts because it shows fins in an undisturbed and unrestored condition. The dorsal fin lies far back on the body behind the anal fin (FH no. 5026, DNHM no. 1667). Length of the dorsal fin base is contained approximately 2 times in height of the anterior ray. The dorsal fin comprises 13-15 rays.

The anal fin lies entirely in front of the dorsal fin. There are 12 anal fin rays (FH no. 5026), but 14 anal pterygiophores indicate that at least 2 more rays must have been present. Twelve anal rays are preserved on DNHM no. 1667 and Oakley Public School no. 13-25. Anal fin rays are flattened distally and longitudinally striate. The

anal fin base is contained slightly more than 2 times in length of the anterior ray.

The caudal fin is broad and deeply lunate. The dorsal half of the fin comprises 10 principal rays (FH no. 5026, DNHM no. 1667, AMNH no. 8443) which are preceded by 10-12 rod-shaped raylets approximately 0.5 cm. in diameter. The dorsal-most principal ray is segmented distally in a zigzag fashion at an acute angle to the long axis of this ray. Other principal rays are segmented similarly and branched distally. Ray 4, 5, and 6, counting ventrally from the dorsal-most principal ray, expand distally and form most of the posterior border of the upper caudal lobe. At their bases the raylets and dorsal-most principal ray splay out over the lateral surface of the caudal vertebrae (KU no. 103, AMNH no. 8443) thus stabilizing the caudal fin base. The lower half of the caudal fin consists of 9 principal rays and 10 raylets.

The elongate, broad-rayed pectoral fin characterizes this genus. Eight or 9 rays are present in this fin (AMNH no. 8443, DNHM no. 1667 show 9; FH no. 5026, AMNH no. 8113, USNM no. 4183 have 8). The first ray reaches 59 cm. in length (FH no. 5026). Succeeding rays diminish rapidly in length and the last measures only one-eighth the length of the first ray. Width of the proximal half of the first ray measures 2.5 times width of the 2nd ray. The leading edge of the first ray is narrow. Dorsal and ventral surfaces of this ray are longitudinally striate. There is no evidence of transverse division. Formation of the first pectoral fin ray by combination of dorsal and ventral elements is demonstrated (KU no. 168, 233) by the fact that these elements may be separated from each other. The lower element is not as broad as the upper and tapers distally into the upper. The ventral surface of the upper element shows an elongate depression with irregular crenulate ridges which match grooves on the dorsal surface of the ventral element. The broad, concave articular facet of the first ray is applied to the uppermost scapular dondyle. The anterior border of the facet projects medially anterior to the scapular facet as a broad hook. The 2nd ray is dorsoventrally thicker than the first and also longitudinally striate. It is not certain whether the 2nd ray is divided longitudinally. Succeeding rays are divided longitudinally and expanded distally. Enlarged hooklike processes for attachment of ventral pectoral fin musculature project ventrally from proximal ends of the 2nd to 8th (or 9th) rays.

The pelvic fin is situated at the beginning of the last quarter of the distance between the pectoral fin base and origin of anal fin. Seven to 9 (YPM no. 2177 has 9; CNHM no. UF973 and CM no. 4101 have 8; SDNHM no. 63.01 has 7) rays form the pelvic fin. The first pelvic fin ray, about one-half the length of the first pectoral fin ray (FH no. 5026), shows no transverse striation. The 2nd distally segmented, pelvic fin ray is half the width of the first. Remaining fan-shaped rays are distally segmented. In life the pelvic fin lay closer to the body wall than is indicated by its position on exhibited specimens.

[*Scales.*] Scales are elongate ellipsoids (Fig. 13,*A*). Mid-body scales (KU no. 238) measure approximately 4-4.5 cm. in height and 2.5-3 cm. in width. Mid-body scales

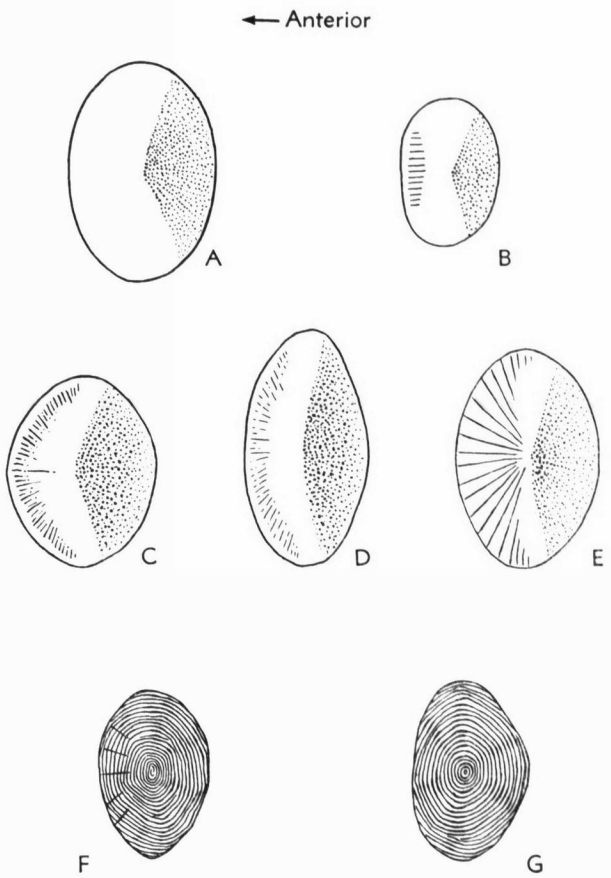


FIGURE 13. Scales of chirocentrid fishes. A. *Xiphactinus audax* LEIDY, Mid-body scale. KU No. 238, ×0.5. B. *Xiphactinus audax* LEIDY. Scale dorsal to operculum. KU No. 11661, ×0.75. C. *Gillicus arcuatus* (COPE). Scale posterior to operculum. KU No. 127, ×0.5. D. *Gillicus arcuatus* (COPE). Mid-body scale. KU No. 143, ×0.6. E. *Ichthyodectes ctenodon* Cope. Mid-body scale. KU No. 11663, ×0.5. F. *Thrissops formosus* AGASSIZ. Mid-body scale. CNHM No. 25341, ×2.0. F. *Chirocentrus dorab* (FORSKÅL). Mid-body scale, ×2.0.

lack anterior radii but are characterized by fine, irregularly distributed punctae on the posterior half. A scale (KU no. 735) from just behind the head is round (Fig. 13,*B*) and 1.5 cm. in diameter. Less than a dozen anterior radii are located in the middle sector of this scale. These radii parallel the long axis of the body.

Discussion. The four species, *Xiphactinus audax, X. mantelli, X. gaultinus,* and *X. australis*, tentatively retained in this revision are distinguished primarily for reasons of geographic and geologic distribution rather than for morphologic differences. Specimens representing European *(X. gaultinus, X. mantelli)* and Australian *(X. australis)* species are fragmentary and of limited number compared to *X. audax*. Characteristics used by original describers to separate species of *Xiphactinus* are not suffi-

ciently consistent from specimen to specimen in the abundant North American collections to warrant application of these characters to geographically widespread representatives of the genus. Investigation of *Xiphactinus* species from outside of North America may support my belief that, despite broad geographic distribution, this genus is represented by a single morphological species.

Six North American species of *Xiphactinus* are placed in synonymy with *X. audax*. Four of them, *Portheus thaumas* (originally *Saurocephalus thaumas,* holotype AMNH no. 1682), *P. molossus* (holotype AMNH no. 1665), *P. lestrio* (holotype AMNH no. 1703), *P. mudgei* (holotype? AMNH no. 1723) were named by COPE. *Saurocephalus thaumas* (COPE, 1870) was transferred (COPE, 1872a) to *Portheus* when COPE distinguished *Saurocephalus* by the presence of foramina on the medial side of each jaw. STEWART (1898b) demonstrated that *P. thaumas* is a synonym of *P. molossus*.

COPE separated his four species by number of premaxillary teeth, size of maxillary and mandibular teeth, as well as shape of the maxillary. Rather than number of teeth, the number of alveoli must be considered, because teeth are generally lost in the process of fossilization. Examination of specimens described by COPE demonstrates that he was actually counting number of alveoli. According to COPE, the number of maxillary alveoli is as follows: *Portheus molossus* has 2 and in a few a smaller 3rd; *P. lestrio* has 3-5, and *P. mudgei* has 4. But the number of premaxillary alveoli may not be the same in both premaxillaries of one individual. For instance, there are 3 alveoli in the left and 2 in the right premaxillary of KU no. 320, MCZ no. 9085 and AMNH no. 1719. Of premaxillaries with 3 alveoli, all alveoli are of equal size or one is larger than the other 2, rather than one being smaller. Furthermore, AMNH no. 1666 labelled by COPE *P. molossus*, has 4 premaxillary alveoli, while AMNH no. 1902, labelled *P. lestrio* has 2 alveoli. Premaxillaries with more than 2 alveoli have relatively longer alveolar borders than those with only 2 alveoli. Also, in specimens with more than 2 premaxillary alveoli, other structures such as neurocrania, mandibles, and maxillaries, on the average measure less than means for these structures. Thus, differences in number of premaxillary alveoli reflect growth stages rather than specific characters of these fishes.

COPE used shape of the maxillary to differentiate *Portheus lestrio* and *P. mudgei*. He characterized the maxillary of *P. lestrio* as "stout and deep with a heavy anterior condyle" (COPE, 1875, p. 193). *P. mudgei* was distinguished by a "thick, shallow" maxillary arch (p. 193). The type maxillary of *P. mudgei* is incomplete. Distortion in the course of fossilization has made it impossible to take natural measurements of this specimen. Maxillaries of *P. lestrio* (AMNH no. 1676) and *P. molossus* (AMNH no. 2373) show similar outlines in dorsal and lateral view. Size of mandibular and maxillary teeth, especially the former, vary from individual to individual, as demonstrated by STEWART. Size of a tooth depends on its stage of development in the replacement series. Characters used by COPE do not serve to distinguish species of *Xiphactinus*.

STEWART named 2 species, *Xiphactinus lowii* (1898a) and *X. brachygnathus* (1899). The holotype of *X. lowii* (KU no. 248), a pair of lower jaws, is distinguished from other species of *Xiphactinus*, according to STEWART, by a short alveolar border and more oblique symphysis. The type and sole specimen was found in the Carlile Shale near Fairbury, Nebraska. A lower jaw of similar profile (KU no. 241) comes from the Niobrara Formation of western Kansas. Length of the *X. lowii* alveolar border is within 1.5 standard deviations of mean alveolar border length given in description of this genus. *Xiphactinus brachygnathus* (holotype KU no. 155, cannot be located in collection) is based on upper and lower jaws and skull fragments. The several characters used by STEWART to distinguish this species, including thickening of premaxillary, shape of maxillary condyle, and short alveolar border are all of a minor nature. Length of maxillary alveolar border falls within 1 standard deviation of the mean for this measurement in *Xiphactinus*. The upper jaw of X. *brachygnathus* figured by STEWART (1900, pl. 45B) resembles that of AMNH no. 1603 (nominally *P. lestrio*) and several specimens previously referred to *P. molossus*. Profile of the mandibular symphysis is similar in its oblique slope to *X. lowii*. STEWART (1900) showed that the shape of the ethmoid and palatine condyles of the maxillary could not be used to distinguish species of *Xiphactinus* as had been attempted by HAY (1898a). STEWART also demonstrated that differences in maxillary and mandibular profile were too variable for use as specific characters.

Examination of numerous *Xiphactinus* specimens has convinced me that characters used by COPE, HAY, and STEWART are inadequate to distinguish species of this genus. No other features indicate taxonomically significant and consistent differences to warrant division of North American *Xiphactinus* specimens into more than one species. Therefore, only *X. audax* is recognized from North America.

I have not seen the following specimens which have been referred to *Xiphactinus*. HILL (1901) referred to *X.* sp. vertebrae identified by LUCAS from the Eagle Ford Shale at its contact with the Austin Chalk southwest of Waco, Texas. STEPHENSON (1912) assigned several teeth from the Snow Hill Marl Member of the Black Creek Formation to *Portheus* sp. These teeth were identified by J. W. GIDLEY. The material is from Kerr's Cove on the Black River, Sampson County, 64½ mi. above Wilmington, Snow Hill, Greene County, and Contentnea Creek, Lenoir County, all in North Carolina. A scale referred to *X. molossus* by MALDONADO-KOERDELL (1956) from the Agua Nueva Formation (upper Turonian) at Xilitla, San Luis Potosi, Mexico, is too fragmentary for positive assignment to this genus.

XIPHACTINUS MANTELLI (Newton), 1877

"unknown fish," MANTELL, 1822, pl. 42, fig. 1, 3, 4.
Megalodon sauroides AGASSIZ, 1835, p. 55.
Megalodon? lewesiensis MANTELL, 1836, p. 30.
Hypsodon lewesiensis AGASSIZ, 1843, p. 99, pl. 25a, fig. 3, pl. 25b, fig. 1-3; BARROIS, 1874, p. 132; GEINITZ, 1875, p 222, pl. 42, fig. 2?

Portheus mantelli NEWTON, 1877, p. 510; WOODWARD, 1901, p. 95; WOODWARD, 1907, p. 101, fig. 29, pl. 21, fig. 8, 9; WOODWARD, 1888, p. 310.

Portheus daviesi NEWTON, 1877, p. 511, pl. 22, fig. 13; WOODWARD, 1901, p. 95; WOODWARD, 1907, p. 102, fig. 30.

Portheus sp. LERICHE, 1902, p. 137; PRIEM, 1908, p. 74; BAYER, 1909, p. 103, 4 figs.

Holotype. Incomplete left maxillary and premaxillary, latter in part and counterpart. Turonian, Lewes, Sussex, England. BMNH no. 4066-4067.

Geologic occurrence and distribution. Cenomanian (lower chalk, Zone of *Holaster subglobosus*): Burnham, Halling, Dover, Kent; Turonian (Middle Chalk, Zone of *Rhynchonella cuvieri*): Burnham, Kent; Cenomanian-Turonian (zones undetermined): Warminster, Wiltshire; Guildford, Surrey; Maidstone, Gravesend, Kent; Lewes, Sussex. ?Lower Senonian (Upper Chalk): Bromley, Kent. All of these English localities are cited by WOODWARD (1901). On continental Europe, *Xiphactinus* has been recorded from the Cenomanian-Turonian near Strehlin, Poland, and near Prague, Czechoslovakia (GEINITZ, 1875, FRITSCH, 1878); upper Turonian-lower Senonian at Cangey, Indre-et-Loire and Notre Dame du Thil, Oise, France (PRIEM, 1908); upper Coniacian (Zone of *Micraster cortestudinarium*): Lezennes, France; Santonian: Lonzée, Belgium (PRIEM, 1908).

Diagnosis. Material inadequate for specific characterization. Perhaps distinguished by profile of maxillary which does not drop sharply posterior to palatine condyle as in *Xiphactinus audax*.

Discussion. Taxonomic history of *Xiphactinus mantelli* was traced by NEWTON (1877). *Portheus daviesi* NEWTON is added to synonymy of *X. mantelli*. The holotype and only specimen referred to *P. daviesi* comprises the anterior half of a maxillary and a centrum (BMNH no. 28388). According to WOODWARD (1907) this maxillary is distinguished by (1) "unusually great depth and relatively long extent of anterior part," (2)a convex oral border and (3)a palatine condyle only slightly raised above dorsal margin of the maxillary. The maxillary fragment measures approximately 8 cm. along the alveolar margin and contains 16 alveoli (NEWTON, 1877). This specimen is too fragmentary to provide sufficient information for specific characterization. If complete, it probably would approach the size of the *X. mantelli* holotype which measures approximately 16 cm. along the alveolar border. Profiles of holotypes of both species are essentially alike if one allows for some reconstruction of *X. mantelli*. Distinguishing features of *P. daviesi* cited by WOODWARD are inadequate to separate North American *Xiphactinus* species. There is no reason to think that these factors would serve to separate English Chalk species. Although the holotype of *P. daviesi* comes from Cenomanian strata and the holotype of *X. mantelli* comes from Turonian strata, specimens referred to the latter species also occur in the Cenomanian. The low maxillary palatine condyle is the only character which can now be used to separate *X. mantelli* from *X. audax*.

The premaxillary and maxillary which FRITSCH (1878) referred to *Hypsodon lewesiensis* measures 30 cm. in length in contrast to 16 cm. for the *Xiphactinus mantelli* holotype. The specimen which FRITSCH (1878, pl. 16) described was found near Prague, Czechoslovakia. This specimen more closely resembles *X. audax* than *X. mantelli*. As in *X. audax*, the upper jaw is robust, teeth are large and of irregular size. The maxillary profile drops sharply posterior to the palatine condyle. Differences between *X. mantelli* and the specimen described by FRITSCH perhaps are related to individual age, but existence of *X. audax* in Europe cannot be excluded until this specimen and additional specimens, if available, are reexamined. WOODWARD (1901) lists 18 specimens of *Xiphactinus* from the English Chalk which he said were of large size resembling *X. molossus* (=*X. audax*). He suggested, however, that these English fishes were probably distinct from North American species.

Morphologic differences between *Xiphactinus mantelli* and *X. audax* are slight. Similarities between the few fragmentary specimens of *X. mantelli* from the English Chalk and contemporaneous deposits on the continent and *X. audax* from North America suggest that a single species of *Xiphactinus* may have been widely distributed in Upper Cretaceous seas. The present separation of *X. mantelli* primarily based on geographic distribution and height of maxillary palatine condyle is maintained tentatively pending reexamination of European specimens.

Tentatively placed in synonymy with *Xiphactinus mantelli* are several references to specimens of this genus from European localities. An incomplete dentary from the late Conician (SORNAY, 1956) of Lezennes, France, originally referred to *Hypsodon lewesiensis* (BARROIS, 1874) was later transferred to *Portheus* sp. (LERICHE, 1902). Jaws, quadrate and other parts identified as *H. lewesiensis* (GEINITZ, 1875) may pertain to *Xiphactinus mantelli*. But some of the material GEINITZ figured (pl. 42, fig. 8, pl. 43, fig. 1) belongs to *Pachyrhizodus*. Teeth assigned to *P. mantelli* (PRIEM, 1908) are from the Santonian (SORNAY, 1956) near Lonzée, Belgium. In the same paper, PRIEM cited other specimens probably referable to *Portheus* from Cangey, Notre-Dame du Thil and Pouilly, France. BAYER (1909) described some fragments of *Portheus* from Vinar, Czechoslovakia. He suggested that specimens described by KIPRIJANOV (1860) as *Saurocephalus affinis* might belong to *Portheus*. Examination of KIPRIJANOV's figures, however, suggests that most of this material is referable to *Protosphyraena*. Teeth are laterally compressed and vertebrae do not show lateral ridge and grooves characteristic of *Xiphactinus*. I have not seen any of the material cited in this paragraph.

XIPHACTINUS GAULTINUS (Newton), 1877

Portheus gaultinus NEWTON, 1877, p. 512, pl. 22, fig. 1-12; WOODWARD, 1901, p. 95.

Holotype. Upper and lower jaws, fragments of neurocranium and isolated vertebrae. Albian, Folkestone, Kent, England. London, Museum of Practical Geology.

Geologic occurrence and distribution. Albian, Folkestone, Kent; Cenomanian, Halling, Kent, England (according to WOODWARD, 1901).

Diagnosis. Palatine head of parethmoid vertical. Ratio of maxillary height at palatine condyle to length of dental border: 3. Profile of maxillary posterior to palatine condyle does not drop sharply.

Discussion. Xiphactinus gaultinus is the earliest representative of this genus. Irregular size of dentition and profile of jaws indicate that this fish belongs to *Xiphactinus*.

However, in two respects the species resembles *Ichthyodectes*. Its features include (1) vertical rather than ventro-anterior orientation of parethmoid, and (2) proportions of centra ridge and grooves in which height of the lateral ridge is equal to width of opening of each groove below or above ridge.

Restoration of the *Xiphactinus gaultinus* head figured by NEWTON (1877, p. 518) is erroneous. The mouth cleft should be directed upward rather than horizontally in all Cretaceous chirocentrids.

XIPHACTINUS AUSTRALIS (Woodward), 1894

Portheus australis WOODWARD, 1894, p. 444, pl. 10, fig. 1.

Holotype. Anterior part of upper and lower jaws and palatine. Upper Cretaceous, Tambo Series, Rolling Downs Formation, Gidgery Creek, near Hughenden, Queensland, Australia. Brisbane, Geological Survey of Queensland (F. 2445).

Geologic occurrence and distribution. Upper Cretaceous, Tambo Series, Rolling Downs Formation: Gidgery Creek and Stewart's Creek near Hughenden, Queensland, Australia.

Diagnosis. Palatine condyle of maxillary not prominent. Teeth of approximately uniform size.

Discussion. This species, as *Xiphactinus mantelli* and *X. gaultinus*, is provisionally distinct from *X. audax* primarily because of its geographic location. The robust dentary resembles that of *X. audax,* while both *X. gaultinus* and *X. australis* have a straight maxillary alveolar border with dentition of relatively uniform size.

In the same publication in which WOODWARD erected *Xiphactinus australis* he described, but left unnamed, a few vertebrae from the same beds. These vertebrae (WOODWARD, 1894, pl. 10, fig. 7) resemble those of *Ichthyodectes* in proportions of lateral ridge and grooves. Several scales (pl. 10, fig. 2-6) from the same locality were named *Cladocyclus sweeti*. These scales probably represent more than one genus. WOODWARD included in *C. sweeti* round scales without structure other than circuli, dorsoventrally elongate scales showing only posterior punctae as in *Xiphactinus*, and others with posterior punctae and anterior radii as in *Ichthyodectes*. Until more complete Australian chirocentrid material is discovered these specimens cannot be positively identified.

With the removal of *Portheus dunedinensis* from the chirocentrids (see section on "Fishes Formerly Considered Chirocentrids") and reassignment of *Ichthyodectes marathonensis* to *Pachyrhizodus* (BARDACK, 1962), the fossil record of Australian chirocentrids consists of the *Xiphactinus* holotype and a head (MCZ no. 5402) which may belong to this species.

Genus ICHTHYODECTES Cope, 1870

Ichthyodectes COPE, 1870, p. 536.

Type-species. Ichthyodectees ctenodon COPE, 1870, p. 536.

Geologic occurrence and distribution. Albian-Senonian, England, Europe; Maastrichtian, Morocco; ?Albian-Campanian, North America.

Diagnosis. Elongate fishes reaching almost 2 m. in standard length. Head contained 6.5-7 times in standard length. Maximum depth of trunk included 6 times in standard length. Supraoccipital crest forms one-third of neurocranial height. Basipterygoid process prominent. Mean angle between otic and orbital sections of parasphenoid 149 degrees. Ventral surface of parasphenoid flat. Intercalar forms only posterior face of hyomandibular fossa. Subtemporal fossa as in *Xiphactinus*. Canal for lateral head vein passes from rear of neurocranium into subtemporal fossa. Mean number of premaxillary alveoli 7 (range 3-12). No premaxillary teeth exceed 1 cm. in crown height. Mean length of maxillary alveolar border 11.2 cm. Maxillary teeth conical, of approximately uniform crown height. Mean number of maxillary alveoli 48 (range 40-58). Mandibular symphysis contained 2.0-2.9 times in length of alveolar border. Mean number of dentary alveoli 31 (range 22-38).

Vertebrae 68-72; 41-44 abdominal, 26-27 caudal. Height of lateral ridge on centra approximately equal to width of groove above and below ridge. Dorsal fin with 10 rays originates posterior to anal fin. Anal fin with ?10-11 rays. Pectoral fin with 8-11 rays. All pectoral fin rays divided longitudinally. Pelvic fin begins in last third of distance between pectoral fin base and origin of anal fin. Mid-body scales twice as high as long, ovate or tapering dorsally and ventrally. Anterior radii less numerous but longer than in *Gillicus*. Posterior punctae less dense than in *Gillicus* and limited to a more central sector of the scale.

ICHTHYODECTES CTENODON Cope, 1870

Text-fig. 13,*E*, 14-16

?Cladocyclus occidentalis LEIDY, 1857, p. 256; LEIDY, 1858, p. 90; LEIDY, 1873, p. 288, 347, pl. 17, fig. 21-22, pl. 30, fig. 5.

Ichthyodectes ctenodon COPE, 1870, p. 536; COPE, 1871a, p. 421; COPE, 1872b, p. 339, 340; ——, 1875, p. 207, 241, pl. 46, fig. 1-4; HAY, 1898b, p. 226; LOOMIS, 1900, p. 244, pl. 23, fig. 7-8; STEWART, 1900, p. 303, pl. 49, fig. 5-7, pl. 51, fig. 12-13; WOODWARD, 1901, p. 100.

Ichthyodectes hamatus COPE, 1872b, p. 339, 340; COPE, 1875, p. 209, 274, pl. 46, fig. 5; HAY, 1898b, p. 225; LOOMIS, 1900, p. 243, pl. 33, fig. 9a, b; STEWART, 1900, p. 298, pl. 48, fig. 2, pl. 50, fig. 1-7.

Ichthyodectes anaides COPE, 1872b, p. 339, 343; COPE, 1875, p. 206, 274, pl. 44, fig. 14, 15, pl. 45, fig. 1-8; CROOK, 1892, p. 111, 123, pl. 15; HAY, 1898b, p. 226, fig. 2; LOOMIS, 1900, p. 244; STEWART, 1900, p. 296, pl. 49, figs. 1-3; WOODWARD, 1901, p. 100; HAY, 1903, p. 54.

Ichthyodectes multidentatus COPE, 1872b, p. 339, 342; COPE, 1875, p. 212, 274, pl. 50, fig. 6-7; HAY, 1898b, p. 227; LOOMIS, 1900, p. 243; HAY, 1903, p. 57, fig. 42.

Ichthyodectes cruentus HAY, 1898b, p. 225, fig. 1, 3, 4; STEWART, 1900, p. 300, pl. 50, fig. 8-10b.

Saurodon pygmaeus LOOMIS, 1900, p. 248, pl. 23, fig. 10.

Ichthyodectes acanthicus? STEWART, 1900, p. 301, pl. 51, fig. 1-11.

Ichthyodectes parvus STEWART, 1900, p. 302.

Holotype. Left maxillary and and posterior three-quarters of right maxillary; left dentary, 2 quadrates, anterior vertebrae. Niobrara Formation, North Fork Smoky Hill River, Logan Co., Kansas, AMNH no. 1910.

Geologic occurrence and distribution. (See list of material examined for specific localities). Carlile Shale, S. Dak.; Eagle Ford Shale, Texas; Niobrara Fm., Kans.; Selma Chalk: Alabama; Pierre Shale: Kansas, Wyo., S. Dak.

Diagnosis. Essentially same as for genus. *Ichthyodectes ctenodon* has 40 or more maxillary alveoli in contrast to 40 or less in *I. minor.*

Material examined. Approximately 75 specimens of *Ichthyodectes* were seen. Only three almost complete, intact skeletons of this genus have been found. The first (USNM no. 12358) comes from the Niobrara Formation (Smoky Hill Chalk Member, 12 mi. SE of Russell Springs, Logan Co., Kans., sec. 16?, T. 15 S., R. 34 W.); this individual, of 155 cm. standard length, lies in an approximately natural position. Dorsal, anal, caudal and pelvic fins are restored. The second (USNM no. 18473) comes from the Pierre Shale (Sharon Springs Member) in Niobrara Co., Wyo. (NE¼, sec. 11, T. 38 N., R. 61 W.). This specimen of 180 cm. standard length is strongly contorted. Dorsal and anal fins are not preserved. The third skeleton (FH no. 8567) from the Niobrara Formation (Smoky Hill Chalk Member) of Logan Co., Kans. (sec. 15-16, T. 15 S., R. 34 W.). This is a young individual of 110 cm. standard length. The posterior part of the head is crushed and all fins restored. Ventral ends of pleural ribs are not preserved, giving this fish an appearance of exaggerated length in proportion to its depth. A fourth skeleton (KU no. 104, from Trego Co., Kans.) is a composite of two individuals.

Heads and neurocrania, plus several jaws and vertebrae known from specific localities, are listed below. All localities are in Kansas unless otherwise stated.

Carlile Shale.
SW¼, sec. 18, T. 120 N., R. 47 W., near Milbank, Grant Co., S. Dak. (heads shown to me by Dr. R. Sloan).
Eagle Ford Shale.
USNM no. 4868, Bosque Farm, Waco, Tex., vertebrae.
Niobrara Formation (Smoky Hill Chalk Member).
Gove Co., Kans.; AMNH no. 8584, NE¼, sec. 26, T. 15 S., R. 31 W. (Haverfield Ranch), mandible; AMNH no. 1633, rear of neurocranium; AMNH no. 2005, head; AMNH no. 1810, neurocranium and jaws.——Graham Co.: AMNH no. 8572, SW¼, sec. 11, T. 8 S., R. 23 W., rear of neurocranium and jaws; AMNH no. 1743, neurocranium, maxillary, pectoral girdle, headwaters of Solomon River (?Graham Co.). Logan Co.: AMNH no. 8573, SW¼, sec. 12, T. 15 S., R. 35 W., premaxillary; KU no. 78, sec. 1, T. 15 S., R. 37 W., parts of neurocranium and jaws; KU no. 12023, sec. 16, T. 14 S., R. 35 W., pelvic girdle.——Trego Co.: KU no. 934, sec. 3, T. 15 S., R. 25 W., pectoral girdle; KU no. 944, W½ sec. 3, E½ sec. 4, T. 14 S., R. 25 W., fin ray fragments; KU no. 357, head.——Additional specimens are from the Niobrara Formation of western Kansas but more precise locality data are unknown: KU no. 117, neurocranium, vertebrae and fin fragments; KU no. 132, rear section of neurocranium; KU no. 597, near section of neurocranium; KU no. 11662, neurocranium, jaws and pectoral girdle; KU no. 12012, neurocranium and jaws; AMNH no. 1622, neurocranium.
Pierre Shale (Sharon Springs Member).
KU no. 89, sec. 18, T. 12 S., R. 36 W., Logan Co., vertebrae; CNHM no. PF 212, 8 mi. S Fairburn, S. Dak., maxillary; AMNH no. 8591, 20 mi. S Edgemont, S. Dak., neurocranium; AMNH no. 8615, sec. 17, T. 38 N., R. 61 W., Niobrara Co., Wyo., head and jaws; SDSM no. 52129, Mule Creek Junction, Wyo., head.

Description. Describers of *Xiphactinus* also reported on *Ichthyodectes.* Reports of Hay (1898b, 1903) and Loomis (1900) were primarily devoted to *Ichthyodectes.* Papers by Cope (1875), Crook (1892) and Stewart (1900) are brief and contribute little to an understanding of differences between *Ichthyodectes* and *Xiphactinus.* Differences between *Ichthyodectes* and *Xiphactinus* are stressed in the following description.

[*Body form.*] Body profile of *Ichthyodectes* resembles that of *Xiphactinus.* The head is contained 6.5-7 times in standard length. On FH no. 8567, the head is contained 7 times in standard length. This is a young individual, as indicated by the large orbit, short mandible (6.7 cm. long) and thinness of head bones. Higher proportions of head length or body depth to standard length are normal in young clupeiforms.

[*Neurocranium.*] Stout, longitudinal ridges on frontal bones give *Ichthyodectes* neurocrania a bulbous appearance above the orbit (Fig. 14). Mean length of 4 neurocrania is 15.9 cm. (range 12.8-19.1, standard deviation 2.9 cm.) measured from anterior end of the vomer to posterior end of the basioccipital. Neurocranial length of FH no. 8567 cannot be determined exactly because the basioccipital is covered. It is approximately 7 cm. long.

The width of the vomer is contained twice in its length. The ventroanterior end of this bone projects anteriorly as a ramlike process (AMNH no. 1611) suggestive of the *Chirocentrus* vomer. An elongate, spatulate patch of chondrified cartilage on the ventral surface of the vomer probably contained fine teeth (KU no. 76). The ethmoid ends ventroanteriorly in a curved beak; not bluntly, as stated by Stewart (1900). The parethmoid shows a dorsoventral groove on the lateral surface posterior to the palatine head. This head is vertical in its orientation, rather than directed ventroanteriorly as in *Xiphactinus.*

Each frontal bears a broad, dorsally flattened ridge (Fig. 15). This ridge, approximately one-half to one-third the width of each frontal, forms a gentle curve extending from posteromedial to anterolateral end of each frontal. A longitudinal, lateral groove at the base of each ridge receives the medial margin of each supraorbital. A median fontanelle between the frontals just posterior to their junction with the ethmoid appears on two specimens (AMNH nos. 1611, 8591).

The supraoccipito-parietal crest rises more sharply than in *Xiphactinus.* The dorsal margin of this crest has a mean angle of 39 degrees (range 35-40 degrees in 4 specimens) to the horizontal body axis. The fused parietals show a reduced (KU no. 357) cluster of small knobs or none (AMNH nos. 1611, 1810) at the mid-sagittal line. The epiotic accessory process is absent or only slightly developed. Subepiotic and post-temporal fossae are proportionally smaller than those of *Xiphactinus.* A foramen for a sensory branch of the 7th nerve (AMNH no. 1611, KU no. 11662) appears on the lateral rather than medial surface of the pterotic.

The shape of the parasphenoid is characteristic of *Ichthyodectes.* Below the orbit this bone is triangular in cross section and its ventral surface is flat, rather than slightly convex. Mean angle formed between suborbital and subotic sections of the neurocranium is 149 degrees (range 145-152 degrees in 4 specimens). Posterior division of the parasphenoid into 2 arms occurs below the middle, rather than below the posterior end of the prootic as in *Xiphactinus.* A stout basipterygoid process is present.

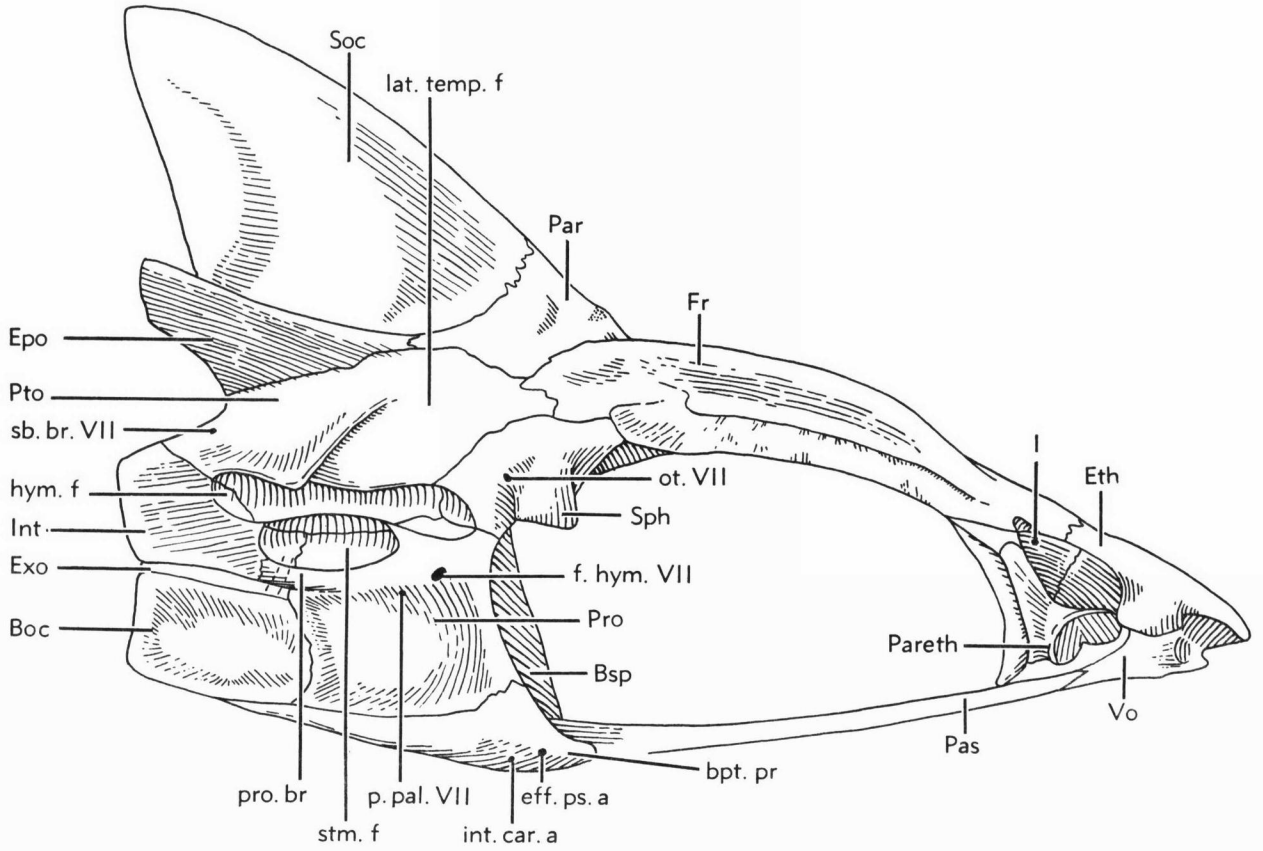


FIGURE 14. *Ichthyodectes ctenodon* COPE. Restoration of lateral aspect of neurocranium. Based on KU No. 11662 and AMNH No. 1611, approx. ×1.0. [For explanation of abbreviations see p. 4.]

The form of the prootic and arrangements of foramina, especially on the posterior face of the orbit, resemble those of *Xiphactinus*. On the lateral prootic surface the foramen for the pretrematic branch of the 7th nerve lies directly (AMNH no. 1611) below the large opening for the hyomandibular branch of the 7th nerve or below and posterior to this foramen (AMNH no. 1810, KU no. 11662).

Pterosphenoid, orbitosphenoid, basisphenoid, and basioccipital are developed as in *Xiphactinus*. Exoccipital foramina for 9th nerve and subtemporal branch of this nerve are not evident. The lateral wall of the large canal through which the 10th nerve and lateral head vein pass is formed by a thin plate of the exoccipital which is covered by intercalar.

The intercalar forms only the posterior corner of the hyomandibular fossa (KU no. 132, AMNH no. 1611). A low, nipple-like protuberance which receives the ventral arm of the post-temporal rises from the posterior surface of the intercalar. The surface of this protuberance is characterized by irregularly crinkled grooves.

In addition to the 2 semicircular sclerotics, the rear of the eye is supported by an osseous cup (KU no. 11662) approximately 2 cm. in diameter. The circumference of this cup is characterized by fine, comblike prongs. A short stem on the medial surface of the cup (KU no. 357) shows 3 canals in cross section. The optic tract or ophthalmic vessels, or both, probably passed through these canals to the eye.

[*Maxillary-mandibular bones.*] The premaxillary is rhomboidal or ellipsoidal in profile (Fig. 16). The anterior margin is thickened and may be notched dorsally (KU no. 87, AMNH no. 2186) or straight (KU no. 357). The dorsal margin is thin. Approximately two-thirds of the premaxillary length is firmly united to the anterolateral surface of the maxillary. Mean length of the premaxillary alveolar border is 2.5 cm. (range 1.5-3.2 cm. in 20 specimens; standard deviation 0.5 cm.). Mean number of premaxillary alveoli is 6.6 (range 3-12 in 20 specimens; standard deviation 2.5). Mean ratio of alveolar length to diagonal height is 56. Premaxillaries with more than mean number of alveoli have a higher than mean ratio of alveolar length to diagonal height.

Premaxillary teeth are conical and approximately 2 mm. in diameter at their bases. Teeth on premaxillaries above mean alveolar border length tend to be anteroposteriorly compressed. Teeth of larger premaxillaries decrease in crown diameter anteroposteriorly. Thus, the first and 3rd teeth of KU no. 357 are 3 mm. in anteroposterior

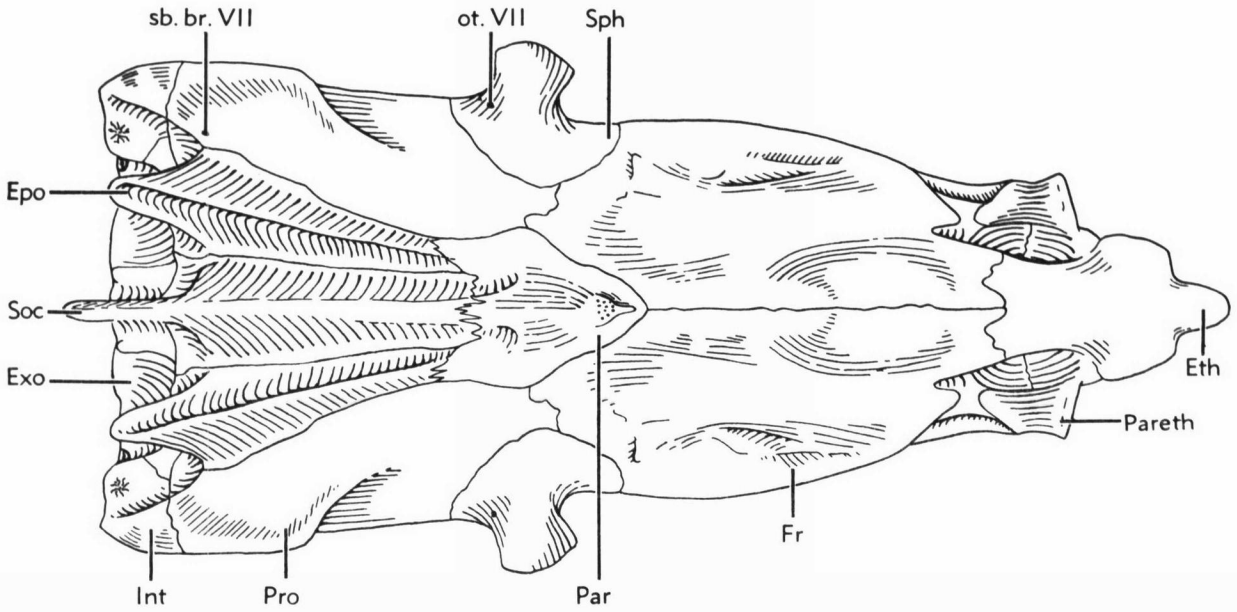


FIGURE 15. *Ichthyodectes ctenodon* COPE. Restoration of dorsal aspect of neurocranium. Based on AMNH No. 1611, approx. ×1.0. [For explanation of abbreviations see p. 4.]

length at the alveolar mouth and 4 mm. in transverse diameter. The 6th and last tooth of this specimen measures 2 mm. in both diameters. Teeth are directed ventroanteriorly in small premaxillaries but ventrally (KU nos. 87, 357) on specimens with large premaxillaries. Of 7 specimens with right and left premaxillaries of one individual, all but 2 differ in number of alveoli on right and left sides. The sequence of alveoli with and without teeth differs on each side of the 5 individuals in which this sequence can be determined.

In profile, dorsal and ventral margins of the maxillary are essentially parallel but not necessarily straight. The posterior end of the maxillary lies behind the orbit. Anteriorly the maxillary curves inward toward the ethmoid. This curve is relatively sharper than in *Xiphactinus*. Because maxillary teeth are of uniform size, the alveolar margin is not swollen. Anterior and posterior condyles on the dorsal surface vary in outlines as in *Xiphactinus*. Maxillaries show their greatest transverse width, approximately 1.5 cm., below the palatine condyle and taper to the alveolar border (KU nos. 78, 180, AMNH no. 1649) or are of uniform thickness (KU nos. 87, 118) of approximately 1 cm. Differences in transverse breadth are not related to number of alveoli or length of maxillary. Fine striae radiate posteriorly and ventrally from the mid-lateral surface of this bone. There are two supramaxillaries.

Mean length of maxillary alveolar border in 17 specimens is 11.2 cm. (range 9.4-13 cm.; standard deviation 1.6 cm.) measured from juncture with premaxillary to most posterior alveolus. Mean height of maxillary at palatine condyle is 3.4 in 29 specimens (range 2.5-4.5 cm.; standard deviation 0.6 cm.). Mean ratio of maxillary height to length is 33 (range 27-39 in 14 specimens).

Smooth, conical maxillary teeth do not exceed 8 mm. in crown height. Diameter of teeth at the jaw margin ranges from approximately 1 mm. in specimens with short maxillaries to 2 mm. in specimens with larger maxillaries. Crown height and diameter at the alveolar mouth gradually diminish posterior to the middle of the jaw. Transverse and anteroposterior diameter of maxillary teeth are equal. Each alveolus lies close to adjacent alveoli without intervening diastemata. The number of maxillary alveoli on right and left sides of the same individual differs in 2 individuals in which this feature can be determined. Mean number of alveoli is 48 (range 40-58 in 17 specimens; standard deviation 4.7).

The mandible includes the same elements as in *Xiphactinus*. The alveolar margin is essentially straight (KU no. 118) on mandibles less than 10 cm. in length. On longer mandibles the alveolar margin rises posterior to the symphysis in some specimens (AMNH no. 1905) forming a pronounced hook. Posterior to this rise the alveolar margin has a gently concave profile which rises gradually to the coronoid process (KU no. 119, AMNH no. 1939). Six to 8 circular depressions on the ventrolateral surface of the dentary starting just behind the symphysis indicate the position of mandibular sensory canal organs.

Mean length of the mandible from ventral end of symphysis to posterior end of dermangular is 13.4 cm. (range 6.7-15.5 cm. in 14 specimens; standard deviation 2.6 cm.). Mean length of symphysis is 3.7 cm. (range 2.0-4.8 cm. in 26 specimens; standard deviation 0.8 cm.). Mean height at coronoid process is 6 cm. (range 5.4-6.5 cm. in 4 specimens; standard deviation 0.5 cm.) from ventral border of the mandible. The anterior margin of the dentary bears a mean angle of 113.6 degrees to the ventral margin

of the dentary (range 103-120 degrees in 14 specimens; standard deviation 4.7 degrees). Mean length of the alveolar border is 9.5 cm. (range 7.5-11.6 cm. in 21 specimens; standard deviation 1.2 cm.).

Mean number of dentary alveoli is 30.6 (range 22-38 in 21 specimens; standard deviation 4.3). Mandibular teeth are conical and curved slightly inward from the vertical plane. On small mandibles, teeth are compressed laterally. Teeth of large individuals may reach 8 mm. in crown height but most are less than 5 mm. high. The number of alveoli on right and left mandibles of one individual differ in the 2 specimens in which the alveoli can be counted. Thus, KU no. 118 has 37 right and 35 left, KU no. 119 has 30 right and 32 left mandibular alveoli.

[*Hyopalatine bones.*] The hyomandibular differs from that of *Xiphactinus* in that (1) the dorsomedial depression below the neurocranial head is oval, rather than triangular, and (2) only a single lateral depression occurs between vertical ridge and opercular head. The metapterygoid does not reach the orbital rim. The dorsoanterior part of this bone is bent laterally and with a dorsoposterior projection of the mesopterygoid forms part of a groove which receives the basipterygoid process. Irregular patches of chondrified cartilage cover the inner surfaces of ecto-, meso-, and perhaps also metapterygoids. Fine teeth, which have not been preserved, probably filled the numerous openings in this cartilage. Mean ratio of height to length of palatine malleolar head is .63.

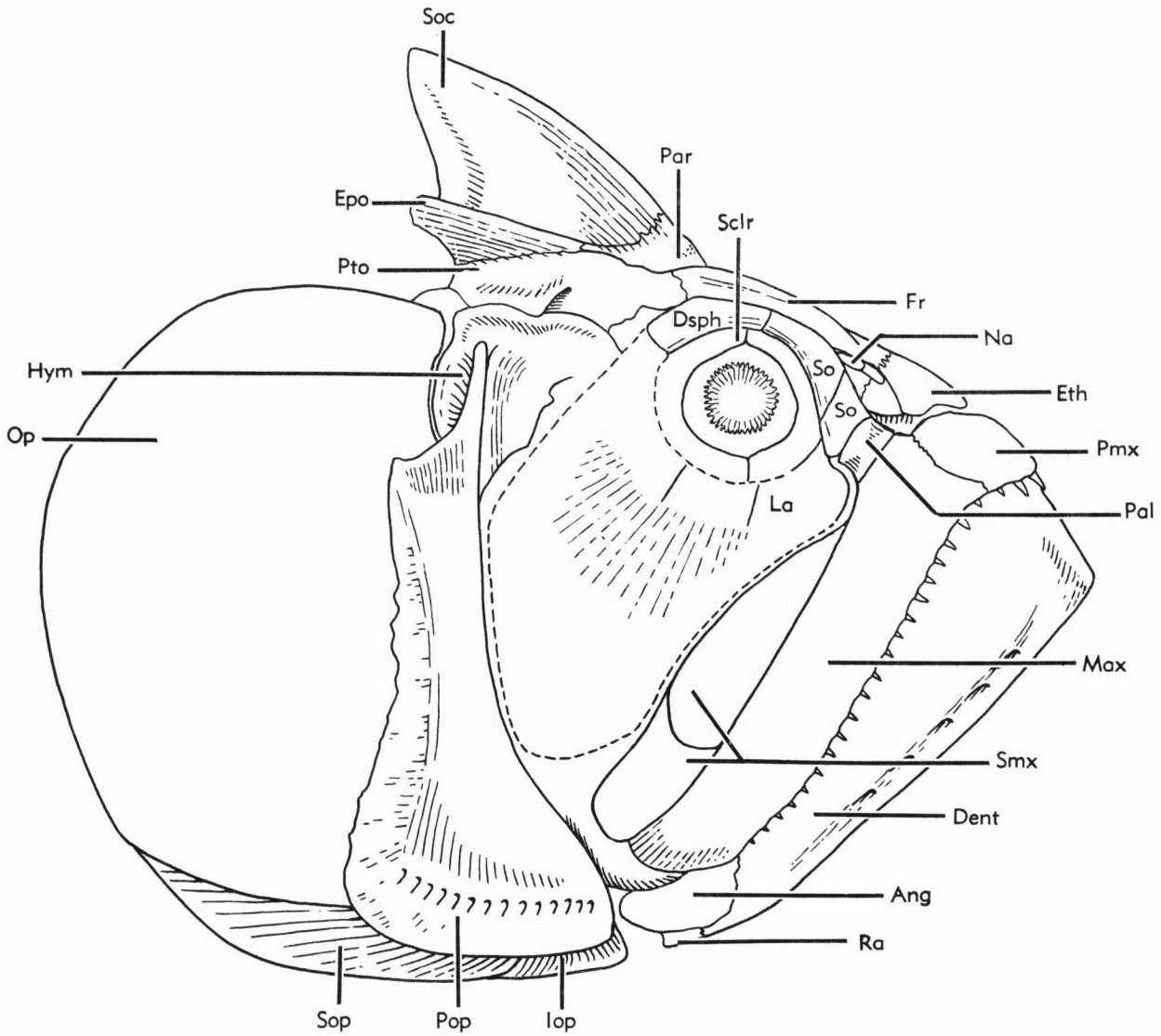


FIGURE 16. *Ichthyodectes ctenodon* COPE. Restoration of head. Based on KU No. 357, ×0.5. [For explanation of abbreviations see p. 4.]

[*Circumorbital bones.*] The posterior supraorbital is strongly convex. The ventral process of this bone is broader and less spikelike than in *Xiphactinus*. A squarish anterior supraorbital covers the remainder of the parethmoid. Number and shape of infra- and postorbitals are uncertain because they are inadequately preserved. Fragments indicate that these bones covered the entire cheek. A pair of nasal bones are present.

[*Opercular bones.*] The posterior margin of the preoperculum is thin and irregularly wavy (KU no. 11666). There are 15 openings for the preopercular sensory canal (KU no. 357). The lateral surface of the operculum is smooth or marked by fine posteroventrally directed lines. There are no completely preserved subopercular. The subopercular surface is characterized by fine posteroventrally directed lines. The only preserved interoperculum (KU no. 11666) is incomplete but probably was ovoid in outline.

[*Hyobranchial bones.*] The ceratohyal is an elongate trapezoidal bone. Least width of the ceratohyal is contained 3.5 times in maximum ceratohyal length. A longitudinal groove is incised on each side of the ceratohyal just above the ventral margin of this bone. Anteriorly these grooves meet and form an elongate fenestra (KU no. 11662). The dorsal edge of the epihyal is straight, while remaining edges, except along the gently sigmoid articulation with the ceratohyal, form a semicircle. A stout, laterally compressed interhyal approximately 1.5 cm. long rises from the epihyal to meet the hyoid arch. The number of branchiostegals exceeds 20, as indicated by still incompletely prepared specimens of *Ichthyodectes ctenodon* shown to me by Dr. Sloan. Cerato- and epibranchials are convex anteromedially and concave posterolaterally. Stout transversely compressed gill rakers reaching 2-3 cm. in length project from the first ceratobranchial. These rakers bear numerous short conical teeth, the largest directed medially.

[*Vertebrae and ribs.*] The vertebral column includes 68-72 centra, of which 41-44 are abdominal and 26-27 are caudal (USNM no. 12358 has 68, 41 abdominal and 27 caudal; USNM no. 18473 has 72; and FH no. 8567 has 70, 44 abdominal and 26 caudal). *Ichthyodectes* centra resemble those of *Gillicus* so closely that isolated centra cannot be distinguished.

The first centrum (KU no. 11662) measures approximately 1 cm. in length and 2.5 cm. in height and width. The front end of the first centrum is nearly flat but the posterior face is deeply concave. Centra dimensions increase rapidly and by the 3rd or 4th measure approximately 2 cm. in length and 3 cm. in height and width. Transverse section (KU no. 11662) of a centrum resembles that of *Xiphactinus*.

A longitudinal ridge first appears on the 4th centrum and gradually reaches full development by the 7th or 8th centrum. This ridge disappears by the 6th from last centrum. A longitudinal groove occurs above and below this ridge. Height of the ridge approximately equals width of opening of either groove. Dorsal depressions for neural arches and ventral pits for hemal arches are present. Each neural arch, from the first to the 16th centrum, joins the arch anterior and posterior to it (USNM no. 12358) in a manner similar to that described in *Xiphactinus*.

The caudal skeleton involves 6 centra, the last 4 of which are turned slightly upward. A separate uroneural (KU no. 11662) must have been attached to the last centrum. This is indicated by the roughened articular facet of this centrum. Hemal spines supporting the caudal fin rays are broad based and swollen. The first hypural, a stout bone, resembles a hemal spine. The 2nd hypural is a broad spatulate bone with a ventroposterior projection at its distal end. The 3rd and 4th hypurals are rod-shaped bones slightly shorter than the 2nd hypural.

Epipleural ribs insert into tear drop-shaped depressions on the longitudinal lateral ridge of each centrum. These depressions are clearly incised on large (KU no. 357) centra but not very distinct on smaller centra (KU no. 104). Epineural ribs arise from bases of the first 36 abdominal centra (USNM no. 12358). More than half of these ribs (exact number cannot be determined) project posteriorly over the neural spines of 10 vertebrae before turning dorsally. Posterior epineurals are directed dorsally and do not overlap neural spines of the next posterior centra. Hemal arches arise on the 24th centrum (USNM no. 12358). Pleural ribs gradually transfer their attachment from parapophyses to hemal arches. Interneural bones have not been seen in *Ichthyodectes*.

[*Pectoral and pelvic girdles.*] The preserved posterior part of the quadrilateral post-temporal (KU no. 11662) resembles that of *Xiphactinus*. There is no evidence of an extrascapula. The supracleithrum is an elongate, thin, rectangular bone with rounded ends. It lies at an angle of approximately 45 degrees to the horizontal body axis. The postcleithrum is similar to that of *Xiphactinus*.

The anterior end of the cleithrum (KU no. 11662) curves ventrally over the forward end of the coracoid. There are no surface markings on the cleithrum. The uppermost of the 3 scapular facets is half the length of the corresponding facet in *Xiphactinus*. The concave middle facet is longer than high or of equal height and length. The lowest facet is slightly convex.

Two hemispherical pockets, one depressed in coracoid alone, the other in scapula and coracoid, face posteriorly from the pectoral girdle. Pectoral actinosts resemble those of *Xiphactinus*.

On the pelvic girdle the protuberance (KU no. 102) between dorsal and ventral facets for the first pelvic fin ray projects relatively more laterally than in *Xiphactinus*.

[*Fins.*] The dorsal fin arises behind the anal fin. At least 10 rays comprise the dorsal fin (KU no. 104). Nine dorsal pterygiophores are preserved on USNM no. 12358. The anal fin ray count is uncertain. Nine anal pterygiophores are present on USNM no. 12358 and at least 8 on KU no. 104.

The caudal fin is similar to that of *Xiphactinus*. There are 10 principal dorsal rays on KU no. 104 preceded by 9 rodlike raylets. The lower rays of the upper lobe are short and distally spatulate.

Eleven pectoral fin rays are present (KU no. 11665 and FH no. 8567). The first ray (USNM no. 12358) measures

approximately 25 cm. in length and is 1.5 times the width of the 2nd. All rays are distally divided both longitudinally and transversely. The pelvic fin (FH no. 8567) has 8 rays.

[*Scales.*] Mid-body scales are dorsoventrally elongate ellipsoids of the same proportions and size as in *Xiphactinus*. About 18 radii are present on the anterior half of each scale (Fig. 13E). These radii, situated mainly in the central sector almost reach the scale nucleus. Punctae on the posterior half of the scale are less dense than in *Gillicus*.

Discussion. Distinction between the North American species *Ichthyodectes ctenodon* and *I. minor* of England and Europe depends primarily on geographic distribution rather than morphologic differences. Characters used by Woodward (1901, 1903, 1907) to distinguish English Chalk species of *Ichthyodectes*, (1) maxillary and mandibular profile, and (2) shape of teeth, are inadequate to distinguish these fishes from North American species.

In this study, seven North American species are placed in synonymy with *Ichthyodectes ctenodon*. Four *Ichthyodectes* species were named by Cope: *I. ctenodon* (holotype, AMNH no. 1910), *I. hamatus* (holotype, AMNH no. 1905), *I. anaides* (holotype, AMNH no. 1939), and *I. multidentatus* (holotype, AMNH no. 2186). Cope (1875) differentiated these species by (1) number of teeth on premaxillary and dentary, and (2) profile of maxillary and mandible alveolar border. Hay (1898b), in addition to using jaw profile, distinguished species of *Ichthyodectes* by counting the number of teeth per inch on jaw fragments. But parts of a jaw which he measured varied from individual to individual. Furthermore, posterior teeth have a smaller diameter at the alveolus than those from middle or anterior end of a tooth row and are more closely spaced. Recently erupted teeth are smaller than older teeth. Therefore, counting number of teeth per inch cannot be used to separate species.

According to Cope, *Ichthyodectes anaides* and *I. hamatus* have 5 premaxillary teeth, while *I. multidentatus* has 12. The holotype of *I. ctenodon* lacks a premaxillary. Cope was actually counting alveoli rather than teeth. The number of premaxillary alveoli tends to differ from one side to the other in the same individual. Thus, NMC no. 8158 has 10 right and 8 left premaxillary alveoli and Loomis (1900, pl. 23, fig. 7) showed a specimen with 7 right and 4 left alveoli. Other individuals differ by one premaxillary alveolus. Variation in number of premaxillary alveoli is correlated with length of premaxillary alveolar border and as a size-related feature cannot be used to determine specific differences. Cope also considered as a specific difference whether the first or 2nd premaxillary tooth is more prominent. The most prominent tooth (and it may be the 3rd as on KU no. 180) is determined by its stage of eruption and its place in the wave of tooth replacement. Individual tooth size is not a specific character.

Similarity of maxillary profiles among the four Cope species is demonstrated by the illustration of Loomis (1900, fig. 9). The strong concave alveolar border exhibited by *Ichthyodectes hamatus* (AMNH no. 1905) resembles that of other specimens identified by premaxillary teeth as *I. anaides* (KU no. 357). On most maxillaries the dental margin is straight (FH no. 8567, KU nos. 87, 104, 11662, AMNH nos. 1743, 1910, 8186). These specimens have been identified as *I. ctenodon, I. anaides,* and *I. multidentatus*. Differences in maxillary profile are the result of individual variation or deformation in the course of fossilization, as may be the case in the holotype of *I. hamatus*.

Mandibular outlines of the four Cope species resemble each other (Loomis, 1900, fig. 8). The hooklike process at the anterior end of the mandible which Cope used to characterize *Ichthyodectes hamatus* is an extreme development, rather than a unique feature, as indicated by the Loomis figures and examination of a series of *Ichthyodectes* mandibles. The number of dentary alveoli is approximately equivalent in 3 of the 4 Cope species for which complete dentaries are preserved. Thus, *I. anaides* has 29 (Cope said 30), *I. hamatus* has 28 (Cope said 25), and *I. ctenodon* has 26.

The holotype of *Ichthyodectes multidentatus* (AMNH no. 2186) comprises a premaxillary and anterior end of maxillary. To judge by color and thickness these bones may not belong to the same individual. The premaxillary represents an extreme in number of alveoli (12) and ratio of alveolar border length to diagonal height of premaxillary (71). Other specimens which include maxillaries and mandibles similar to those of *I. ctenodon* have premaxillaries with 10 or 11 alveoli and a higher than mean ratio of alveolar border length to diagonal height. Therefore, *I. multidentatus* can be referred to *I. ctenodon*.

Ichthyodectes prognathus (Cope) was originally referred to *Saurocephalus* (Cope 1870) but later transferred to *Ichthyodectes* (Cope 1872b). Examination of the holotype (AMNH no. 1912) shows that the first determination was correct. The premaxillary resembles that of *Saurocephalus*. The anterior border of this bone is straight and not thickened above the alveolar border. Alveoli extend onto the medial surface and the sole preserved tooth is laterally compressed rather than round.

The holotype of *Ichthyodectes cruentus* Hay is an incomplete maxillary, which, judging from the figures (Hay, 1898b, fig. 1, 3, 4), might be represented by AMNH no. 1649. In dorsal and profile views, this maxillary fragment resembles *I. ctenodon*. *Saurodon pygmaeus* Loomis (holotype, Bayerische Staatssamlung, no. 1893X43) lacks medial foramina and must be referred to *Ichthyodectes*. However, teeth of this specimen are slightly compressed laterally, rather than round. Stewart (1900) assigned a premaxillary, maxillary, mandible, and other fragments (KU no. 118) to *I. acanthicus* Cope but, noting that this material might differ from the poorly characterized *I. acanthicus*, suggested a new name, *I. parvus*. Only maxillary and mandible can now be located. *I. acanthicus* Cope pertains to *Gillicus*. Jaws of the Stewart material resemble that of *Saurodon pygmaeus* and other *Ichthyodectes* specimens.

Cladocyclus occidentalis (holotype, Philadelphia Academy of Natural Sciences, no. 5348) is tentatively included in the synonymy of *Ichthyodectes ctenodon*. According to Leidy, this specimen, a scale, came from Nebraska, but

the caption of the figure (LEIDY, 1873, pl. 30, fig. 5) reads Sage Creek, Dakota. Similarly formed scales occur in the Milbank, South Dakota material shown to me by Dr. SLOAN. This material is from the Carlile Shale from which perhaps the LEIDY specimen, preserved in a similar matrix, was obtained. The scale is ovate in outline, tapering dorsally and ventrally. It is 5.5 cm. high and 3.5 cm. long. The anterior region exhibits long radii extending almost to the scale nucleus. Punctae are large and spread over the posterior sector. Pending discovery of such large scales in association with definite *Ichthyodectes* jaws or neurocrania, assignment to *Ichthyodectes* remains tentative. The species *I. occidentalis*, as used by LOOMIS (1900), includes both *Cladocyclus occidentalis* LEIDY and material pertaining only to *Gillicus arcuatus*.

After examination of most of the *Ichthyodectes* specimens from North America, I believe that only one species, *I. ctenodon*, can be distinguished in the Cretaceous deposits of this continent.

Not included in the synonymy of *Ichthyodectes ctenodon* are 6 references to *Ichthyodectes* sp. *I.* sp. HILL (1901) represents vertebrae identified by LUCAS. This material came from the Eagle Ford Shale southwest of Waco, Texas. COCKERELL (1919) assigned two scales to *I.* sp. One is from the lower part of the Colorado Shale, north of Lower Sherbourne Lake, Montana (USGS Loc. no. 2402) and the other from the Niobrara Formation, 3-4 mi. S of Butler, North Park, Colorado (USGS Loc. no. 7277). These dorsoventrally elongate, lateral line scales with numerous anterior radii are less than 6 mm. high, seem to lack anterior punctae, and probably do not pertain to *Ichthyodectes*. *I.* sp. REESIDE (1923) is a scale (USNM no. 10771) with several long, uninterrupted anterior radii and a few posterior punctae. If correctly identified, this scale from the South Platte Formation (WAAGE & EICHER, 1960) near Bellvue, Colorado is the earliest record of this genus in North America. DAVID (1946) referred a scale fragment from a well core in the Upper Cretaceous Panoche Formation near Chowchilla, California, to *I.* sp. A section of caudal vertebrae and pectoral fin fragments from the Agua Nueva Formation (upper Turonian) near Xilitla, San Luis Potosi, Mexico (MALDONADO-KORDELL, 1956) is inadequate for generic identification. *Ichthyodectes* sp. (ZANGERL & SLOAN, 1960) is based on vertebrae from Milbank, S. Dak. Dr. SLOAN has shown me 2 still unprepared skulls and a trunk fragment all referable to *I. ctenodon* from the same South Dakota locality.

ICHTHYODECTES MINOR (Egerton), 1850

Hypsodon lewesiensis AGASSIZ, 1837, pl. 25a, fig. 5, 6.

Cladocyclus lewesiensis AGASSIZ, 1844, p. 8, 103; WOODWARD, 1888, p. 326; WOODWARD, 1901, p. 109; LERICHE, 1902, p. 137 *(Cladocyclus?)*

Hypsodon minor EGERTON in DIXON, 1850, p. 14, pl. 32*, fig. 9.

Ichthyodectes minor NEWTON, 1877, p. 520, pl. 22, fig. 14; WOODWARD, 1901, p. 102; WOODWARD, 1903, p. 96, fig. 23, pl. 19, fig. 6(?).

Ichthyodectes elegans NEWTON, 1877, p. 512, pl. 22, fig. 15; WOODWARD, 1901, p. 103, pl. 9, figs. 4, 5; WOODWARD, 1907, pl. 97, fig. 24.

Ichthyodectes tenuidens WOODWARD, 1901, p. 104, pl. 9, fig. 6; WOODWARD, 1907, p. 98, pl. 21, fig. 7.

Holotype. Imperfect mandible. Probably from a Turonian zone (WOODWARD, 1903) (BMNH no. 28894).

Geologic occurrence and distribution. Albian, Folkstone, Kent; Cenomanian (Zone of *Holaster subglobosus*), Dorking, Surrey; Bonham, Dover, Upper Halling, Maidstone, Kent; Turonian (zone unidentified), Kent, Surrey, Sussex (above localities from WOODWARD, 1901, 1903, 1907); Senonian: Anzin, Lezennes, France (LERICHE, 1902).

Diagnosis. Material insufficient to characterize this species. Separation of *Ichthyodectes minor* from *I. ctenodon* is maintained primarily for reasons of geographic location. Also, *I. minor* has ?40 or fewer maxillary alveoli.

Discussion. The name *Hpysodon lewesiensis* AGASSIZ, was used in such a broad sense that specimens originally included in this species were divided among 2 genera of elopids and 2 of chirocentrids by WOODWARD (1901). He did not consider *Hypsodon* a valid name for any fish. COPE (1875) and NEWTON (1877) noted that *Hypsodon* included 2 chirocentrid genera. COCKERELL (1919) attempted to resurrect the name *Hypsodon* for a chirocentrid but included *Gillicus*, a genus in no way suggested by material described or figured by AGASSIZ. Of *H. lewesiensis* specimens figured by AGASSIZ, only scales (1837, pl. 25a, fig. 5, 6) pertain to *Ichthyodectes*. He described these scales subsequent to other material included in *H. lewesiensis*. AGASSIZ later (1844) substituted the name *Cladocyclus lewesiensis* for these scales. The generic name *Cladocyclus* applies only to South American chirocentrids. WOODWARD (1903) assigned the English specimens of *C. lewesiensis* to *Ichthyodectes*. Although priority would require that English and European species of *Ichthyodectes* be named *I. lewesiensis*, there is no specimen showing scales and jaws of one individual. Such association would be necessary for positive identification of these scales. Therefore, *I. minor*, represented by an imperfect mandible, the earliest named specimen positively identifiable as *Ichthyodectes* is taken as the specific name for this species.

English *Ichthyodectes minor* specimens consist of one head, several incomplete upper and lower jaws and scales. WOODWARD, who last reviewed these fishes (1903-1907), distinguished species of *Ichthyodectes* by shape of the mandibular dental border and size of mandibular teeth. Study of North American *Ichthyodectes* specimens shows that these features cannot be used to separate species.

The mandible of *Ichthyodectes minor* (holotype, BMNH no. 28894) is characterized, according to NEWTON (1877), by a nearly straight dental border and symphysis approximately one-quarter the length of mandibular ramus. There are 33 alveoli in the incomplete specimen. Teeth are straight. He thought that these characters differentiated *I. minor* from all North American species of *Ichthyodectes* but a straight alveolar border, similar proportions of symphysis and straight teeth are seen on KU nos. 87, 91 among other specimens from the Niobrara Formation.

The holotype of *Ichthyodectes elegans* (BMNH no. 41687) is a dentary with 40 alveoli characterized (NEWTON, 1877) by a concave alveolar margin rising to a "beak-like" symphysis. Teeth are inclined slightly forward. *Ichthyodectes tenuidens* (holotype, BMNH no. 49054) is based on a head and jaws. The large orbit, thin, incom-

pletely ossified bones and narrow, spikelike teeth indicate that this is a young individual. Mandibular profile is similar to that of *I. elegans* and *I. minor*. The narrow, elongate maxillary resembles that of BMNH nos. 5644, 5645, nominally *I. elegans*. Differences in jaw shape are less pronounced in English than in North American *Ichthyodectes*. I believe that *I. elegans* and *I. tenuidens* are synonymous with *I. minor*.

Included in synonymy as *Ichthyodectes* sp. are scales which have been called *Cladocyclus lewesiensis* (Woodward, 1888, 1901, and Agassiz, 1844) or *Hypsodon lewesiensis* (Agassiz, 1837). These dorsoventrally elongate scales with less than 2 dozen anterior radii and many posterior tubercles differ from those of *Gillicus* in which anterior radii are not continuous. European scales referred to *Cladocyclus lewesiensis* (Leriche, 1902) were not figured. Leriche said that they agree with *Cladocyclus* scales from England and Europe. Arambourg (1952) described a few vertebrae from the Maastrichtian of Ouled Abdoun, Morocco (pl. 37, fig. 31) which he referred to *I.* sp. These centra resemble those of saurocephalids more than chirocentrids.

Genus GILLICUS Hay, 1898

Gillicus Hay, 1898b, p. 230.
Type-species. Portheus arcuatus Cope, 1875, p. 204.
Geologic occurrence and distribution. Albian, England; ?Albian-Campanian, North America.

Diagnosis. Elongate fishes attaining standard length of less than 2 m. Head contained approximately 6.5 times and maximum depth of trunk approximately 6 times in standard length. Supraoccipital crest equal to one-half neurocranial height. Fused parietals form low hump medially. Parasphenoid quadrilateral in cross section suborbitally. Basipterygoid process prominent. Mean angle between otic and orbital parts of parasphenoid 130 degrees. Intercalar forms approximately one-quarter of hyomandibular fossa. Subtemporal fossa as in *Xiphactinus*. Canal for lateral head vein passing from rear of neurocranium into subtemporal fossa. Premaxillary with 10-17 alveoli. Premaxillary teeth less than 3 mm. in crown height. Saber-shaped maxillary ends below middle of orbit. Maxillary teeth minute; approximately 150 alveoli. Mandibular symphysis nearly vertical; symphysis contained 1.4-1.7 times in length of mandibular alveolar border. Dentary with approximately 65 minute, alveoli. Mandibular teeth curved slightly inward. Vertebral column with approximately 70 centra. Height of lateral ridge of each centrum about equal to width of groove above and below ridge. All rays of pectoral fin divided longitudinally. Pelvic fin begins in last sixth of distance between pectoral fin base and origin of anal fin. Scales circular or dorsoventrally ovoid. Dense rows of punctae on posterior half of scales. Anterior half with long and short radii. Many long radii not continuous through their length.

GILLICUS ARCUATUS (Cope), 1875

Text-figures 13,*C,D*, 17-21

Portheus arcuatus Cope, 1875, p. 193, 204, 274.
Ichthyodectes acanthicus Cope, 1877, p. 177.
Ichthyodectes arcuatus Cope, 1877, p. 177; Cope, 1892, p. 942.
Ichthyodectes polymicrodus Crook, 1892, p. 112, pl. 16; Crook, 1892, p. 942.
Gillicus arcuatus Hay, 1898b, p. 228, 230; Stewart, 1900, p. 307, pl. 52-54.
Gillicus polymicrodus Hay, 1898b, p. 228, 230.
Ichthyodectes occidentalis (Leidy), Loomis, 1900, p. 242, pl. 23, fig. 1-6.
Hypsodon audax Cockerell, 1919, p. 177, pl. 32, fig. 8(?), pl. 33, figs. 1, 2.
Holotype. The specimen which Cope (1875) described cannot be located in the American Museum Cope Collection. Among the material in the Cope Collection a satisfactory lectotype is AMNH no. 2326, comprising a neurocranium, maxillary, mandible, quadrate and vertebrae from the Niobrara Formation of Gove Co., Kansas.
Geologic occurrence and distribution. (See list of material examined for specific localities). Carlile Shale, Minnesota, South Dakota; Austin Chalk, Texas; Niobrara formation, Kansas; Pierre Shale, Wyoming.

Diagnosis. Mouth cleft inclined upward. Orbit longer than snout.

Material examined. One specimen (FH no. 5026) of *Gillicus arcuatus* is more or less complete. This fish, 161 cm. in standard length, is contained within the abdominal cavity of a *Xiphactinus audax*. Dorsal and anal fins are missing. Paired fins, pectoral girdle and much of the lower part of the head are destroyed.

Heads, neurocrania, plus several jaws and vertebrae known from specific localities are listed below. All specimens are from Kansas unless otherwise stated.

Carlile Shale.
SW¼ sec. 18, T. 120 N., R. 47 W., Grant Co., S. Dak., and NE¼ SW¼ sec. 15, T. 120 N., R. 45 W., Lac Qui Parle Co., Minn. (scales and pectoral fin shown to me by Dr. R. Sloan).

Austin Chalk.
UT 31051, Savoy Pit, Fannin Co., Tex. (locality described by Springer, 1957) vertebrae and caudal fin.

Niobrara Formation (Smoky Hill Chalk Member).
Gove Co., Kans., KU no. 3, T. 13 S., R. 26 W., neurocranium; AMNH no. 8178, neurocranium and vertebrae; AMNH no. 8582, sec. 26, T. 14 S., R. 31 W., neurocranium; CMNH no. 10118, sec. 16, T. 13 S., R. 20 W., neurocranium.——Graham Co., Kans., KU no. 11667, sec. 10, T. 8 S., R. 23 W., neurocranium.——Logan Co., Kans., KU no. 134, near Russell Springs, neurocranium; KU no. 965, Elkader, hind section of neurocranium; KU no. 11669, SE¼ sec. 11, T. 15 S., R. 35 W., mandibles; AMNH no. 8586, sec. 8, T. 15 S., R. 34 W., neurocranium; AMNH no. 8587, sec. 8, T. 15 S., R. 34 W., neurocranium and maxillary; AMNH no. 8588, NE¼ sec. 26, T. 14 S., R. 31 W., neurocranium and maxillary; AMNH no. 8589, SW¼ sec. 12, T. 15 S., R. 35 W., neurocranium and palate.——Trego Co., Kans., KU no. 738, sec. 16 or 21, T. 11 S., R. 24 W., neurocranium, maxillary and fragment of palatine; KU no. 346, W½ sec. 3, E½ sec. 4, T. 14 S., R. 25 W., pectoral girdle; KU no. 10321, sec. 16 or 21, T. 11 S., R. 24 W., neurocranium, premaxillary, hyopalatine fragments; AMNH no. 8603, neurocranium; USNM no. 21081, sec. 16 or 21, T. 11 S., R. 24 W., head.——The following specimens are from the Niobrara Formation of western Kansas but more precise locality information is unknown: KU no. 127, neurocranium and jaws; KU no. 129, neurocranium, premaxillary, maxillary; KU no. 133, neurocranium; KU no. 135, neurocranium, jaws, parts of palate, pectoral girdle and fin; KU no. 138, neurocranium; KU no. 143, neurocranium, jaws, palate, scale; KU no. 146, neurocranium, operculum, incomplete vertebral column; KU no. 339, hind part of neurocranium, pectoral girdle and pectoral fin; KU no. 478, neurocranium; KU no. 80, neurocranium.

Pierre Shale (Sharon Springs Member).
Niobrara Co., Wyo., AMNH no. 8599, SE¼ sec. 2, T. 38 N., R. 61 W., neurocranium and jaws; AMNH no. 8617, sec. 2, T. 38 N., R. 61 W., head; USNM no. 18319, NE¼ sec. 12, T. 38 N., R. 61 W., incomplete head and vertebrae; USNM no. 18347, sec. 12, T. 38 N., R. 61 W., head.

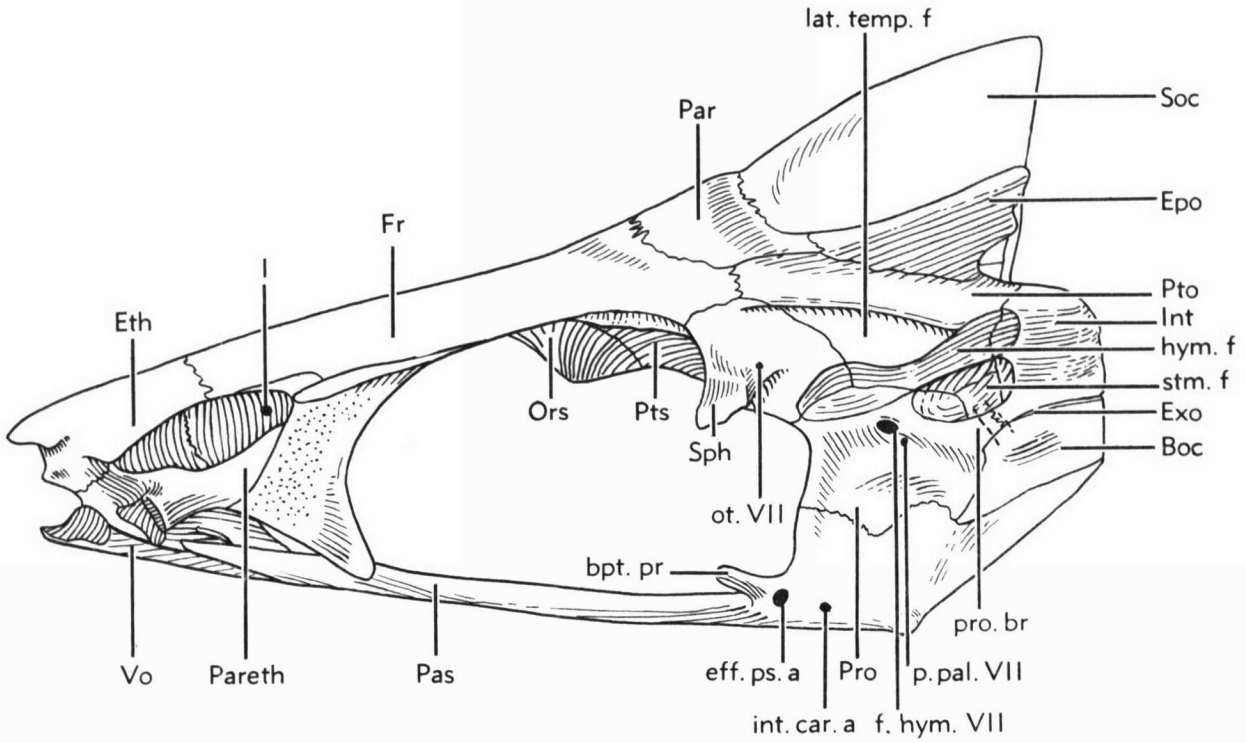


FIGURE 17. *Gillicus arcuatus* (COPE). Restoration of lateral aspect of neurocranium. Based on KU No. 3 and No. 480, ×1.0. [For explanation of abbreviations see p. 4.]

Description. COPE (1875) originally described this genus from fragments of jaws, palatine and vertebrae. CROOK (1892) provided a brief description of complete cranial and postcranial structures. His interpretation of neurocranial and pectoral girdle anatomy parallels his account of *Xiphactinus* and duplicates errors made in description of that genus. HAY (1898b) rectified these anatomical inaccuracies and provided a short account of *Gillicus* within limits of the few specimens at his disposal. LOOMIS (1900) and WOODWARD (1901) included *Gillicus* in *Ichthyodectes*, thus minimizing differences between these two fishes. STEWART (1900) described *Gillicus* material at the University of Kansas Museum of Natural History, offering essentially the same account as that of HAY. Since 1900 *Gillicus* material has accumulated in the Kansas vertebrate paleontological collection. The following description is concerned with structures of *Gillicus* which differentiate this genus from *Xiphactinus* and *Ichthyodectes*.

[*Body form.*] The head is contained 6.5 times in standard length (FH no. 5026). Maximum body depth is included 6 times in standard length. The laterally compressed body with straight dorsal and ventral margins resembles that of *Xiphactinus*.

[*Neurocranium.*] The neurocranial profie of *Gillicus* is characterized by sharp flexure of parasphenoid, anterior projection of parethmoid palatine head and relatively low supraoccipital crest (Fig. 17). Ventral to the hyomandibular fossa the neurocranium is compressed laterally to a greater degree than in *Xiphactinus* and *Ichthyodectes*. Neurocranial ossification is relatively thinner. Mean length of 5 neurocrania is 13.9 cm. (range 7.5-19 cm.; standard deviation 2.2 cm.) measured from anterior end of vomer to posterior end of basioccipital.

The vomer, 3 times longer than wide, projects posteriorly between anterior arms of the parasphenoid and ends below the orbit. The anterior projection of the vomer has a shallow mid-sagittal cleft. Lateral surfaces of this projection are flattened facets continuous with anteriorly directed oval facets of the vomer. The vomer is broadest between parethmoids. Shallow excavations on the ventral vomerine surface indicate where ligaments arose to unite palatines to the neurocranium. The ethmoid lacks the ventrolateral facet which in *Xiphactinus* is continuous with the anterior, oval vomerine facet.

The palatine head of the parethmoid projects more anteriorly than in *Xiphactinus*. A shallow groove on the dorsal surface of the parethmoid runs anteromedially into the nasal capsule. The parethmoid joins the ethmoid in a denticulate suture below the anterior end of the nasal capsule. The parethmoid malleolar head, to which the palatine is articulated, is transversely ovoid. Ventromedial to this ovoid head an ellipsoidal convex facet contiguous with the ovoid head is directed laterally. The medial surface of the palatine malleolus abuts on this facet. Posterior to this ellipsoid facet a short, convex facet receives a dorsal projection of the palatine malleolus. Lateral expansion of the

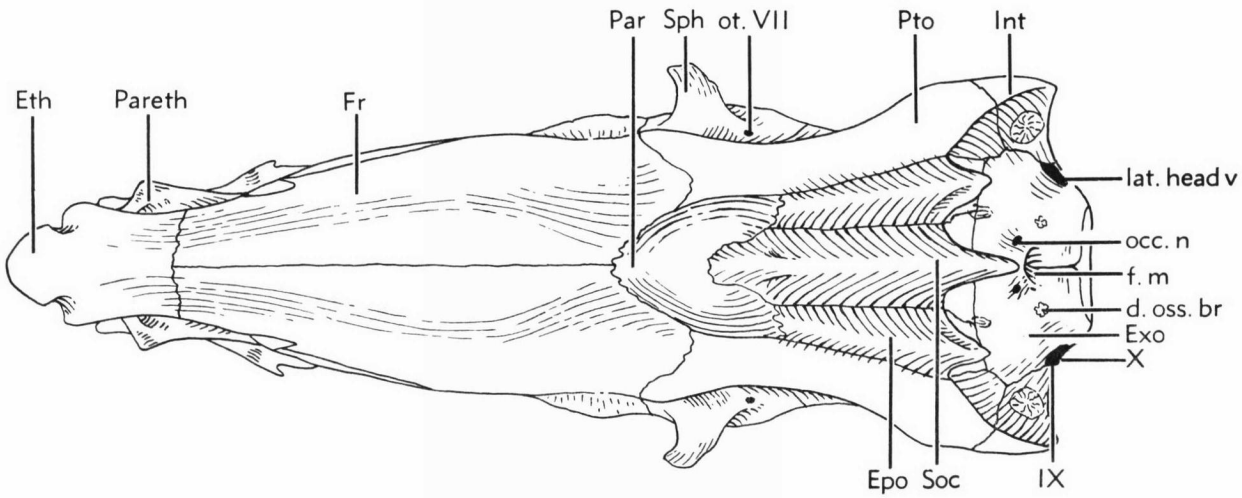


FIGURE 18. *Gillicus arcuatus* (COPE). Restoration of dorsal aspect of neurocranium (based on KU No. 965 and AMNH No. 8603), ×1.0. [For explanation of abbreviations see p. 4.]

dermal section of the parethmoid is proportionally greater than in *Xiphactinus* or *Ichthyodectes* (Fig. 17). The lunate orbital border of this section ends in a ventroposterior projection. The lateral surface of this section is characterized by numerous fine foramina. These foramina lead into dorsoposteriorly directed grooves.

Some *Gillicus* specimens (KU no. 10321, AMNH no. 8603, USNM no. 21081) show a weak ridge on the frontal bones (Fig. 18). In most individuals frontals are flat. Above the orbit, the lateral margin of each frontal is straight. Minute pits of the sensory canal system are especially numerous medioanteriorly (KU no. 138, AMNH no. 8603). The lateral process of the sphenotic is twisted ventrally.

Supraoccipital crest height (AMNH no. 8178, KU no. 480) is contained twice in posterior height of neurocranium. Mean angle formed by supraoccipital crest and horizontal body axis is approximately 23 degrees (range 19-30 degrees in 17 specimens). An anterior projection of the supraoccipital extending below the fused parietals does not reach the frontals (KU no. 965). Parietals form a gentle hump as they rise over the supraoccipital toward the mid-sagittal line. Parietals meet the supraoccipital posterior to this hump in an interdigitating suture.

The epiotic attains one-half supraoccipital crest height. A thin accessory process projects rearward from the lateral face of the epiotic crest. A pair of medially directed ridges arise from the epiotic and contribute lateral support to the supraoccipital crest. The subepiotic fossa is dorsoventrally elongate (KU no. 480).

The pterotic is essentially similar to that of *Xiphactinus*. The dorsal border of the pterotic flange, which limits the lateral temporal fossa medially, curves laterally, thus forming a partial roof to this fossa. A foramen for a sensory branch of the 7th nerve opens from the lateral surface of the pterotic (KU no. 965).

Shape and angle of parasphenoid is characteristic of *Gillicus*. This bone is roughly quadrilateral in cross section below orbit. A sharp corner marks mid-dorsal line and lateral edges. The ventral surface is convex below the middle of the orbit and beneath its anterior end is a longitudinal ridge. The suborbital part of the parasphenoid lies at a mean angle of 130 degrees (range 124-133 degrees in 17 specimens) to the subotic section of the neurocranium. The base of the otic section of the neurocranium angles anteroventrally from the horizontal body axis. Anterior projections of the parasphenoid extend along either side of the vomer and meet the base of the parethmoid. The parasphenoid divides into two wings ventral to the prootic foramen for the hyomandibular branch of the 7th nerve. These wings reach the ventroposterior end of the neurocranium. Viewed ventrally these wings are thin and the space between them continuous with the myodome canal. In lateral view the wings are expanded to form the posterolateral wall of the myodome canal (KU no. 3). The ascending process of the parasphenoid (KU nos. 3, 143) is a long plate which forms the lower half of the anterior myodome wall. The ascending process is proportionally larger than in *Xiphactinus* or *Ichthyodectes*. At the juncture of otic and orbital sections, the parasphenoid is later-

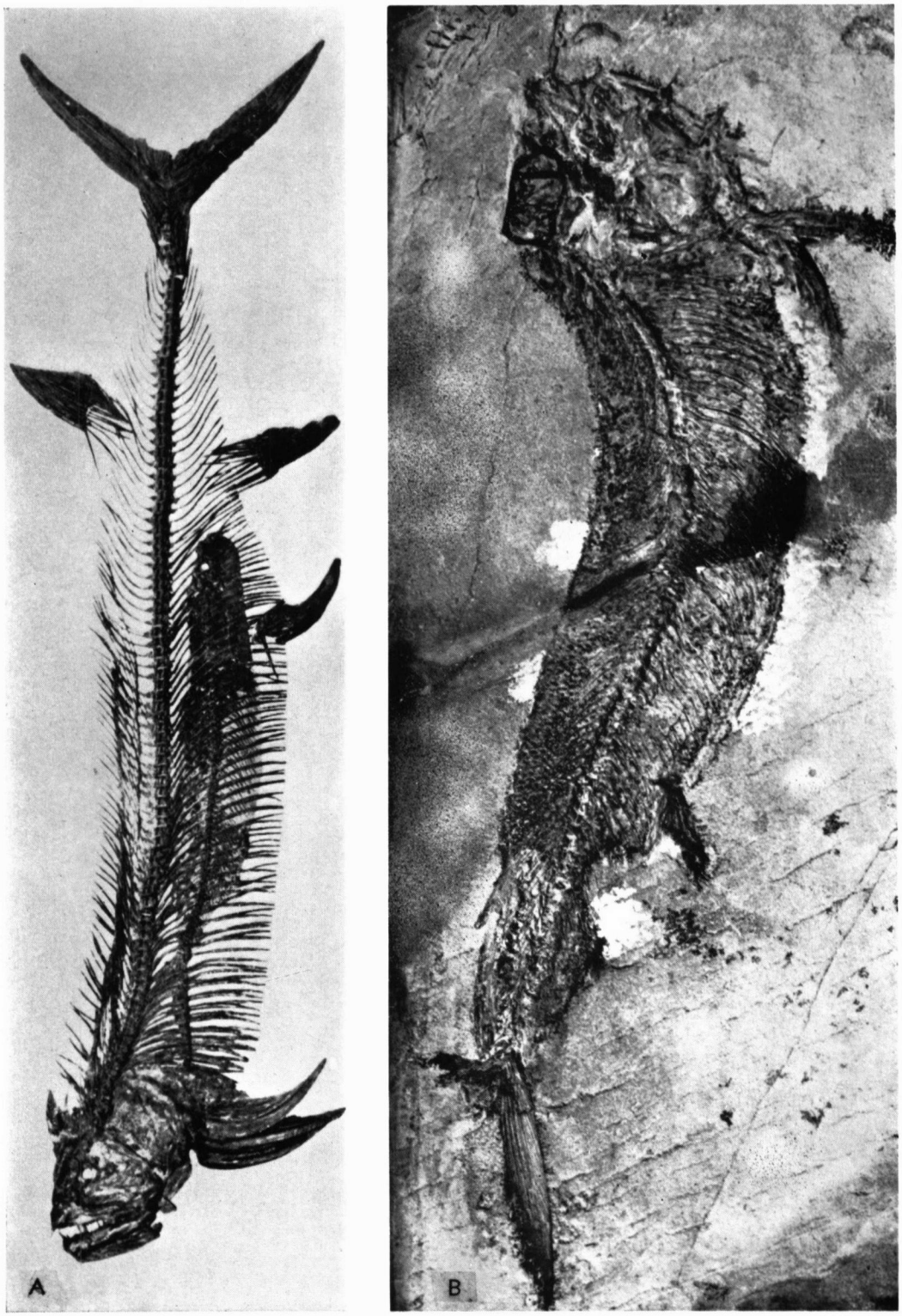
EXPLANATION OF PLATE 1

XIPHACTINUS, PRYMNETES

FIGURE

A. Xiphactinus audax LEIDY. Largest complete specimen. A fish identified as *Gillicus arcuatus* is contained within the abdominal cavity of the large fish. FH no. 5026, approx. ×0.04.

B. Prymnetes longiventer COPE. Holotype. USNM no. 4090, approx. ×0.3. (Photograph courtesy of Dr. C. L. Gazin, USNM.)


A
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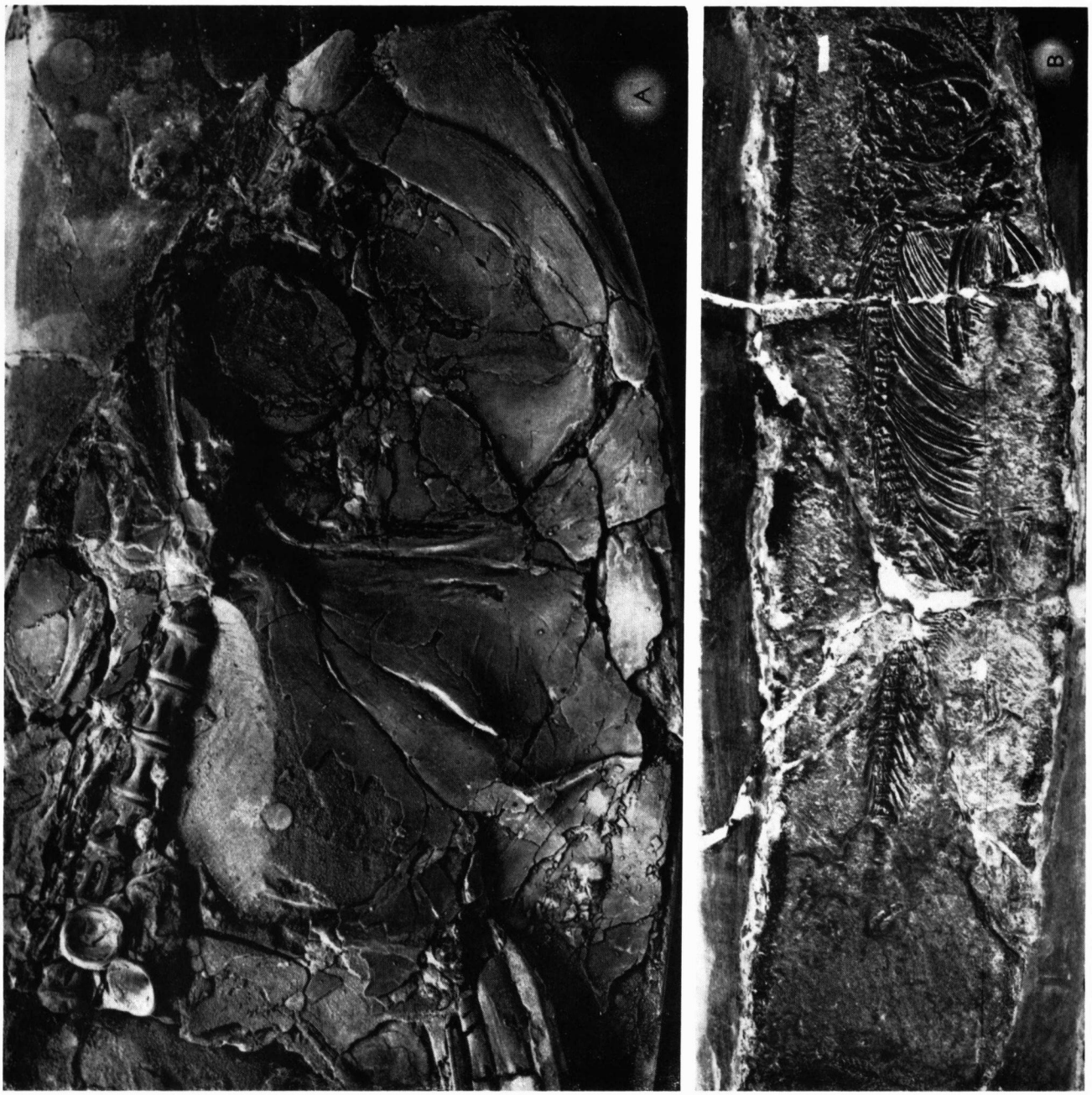
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ally compressed and a short, round swelling projects laterally from this region (KU nos. 3, 480). A basipterygoid process extends anterolaterally from the base of the ascending process. In *Ichthyodectes* and *Xiphactinus* the basipterygoid process arises from the shaft of the parasphenoid. A foramen at the base of the process transmitted the efferent pseudobranchial artery. A smaller, posterior foramen carried the internal carotid artery. On one side of KU nos. 3 and 480 a third foramen appears behind the opening for the internal carotid artery. It probably served for passage of an accessory carotid vessel.

The prootic comprises only half of the lateral neurocranial wall. A large foramen for the hyomandibular branch of the 7th nerve appears on the lateral wall of the prootic and a smaller foramen ventroposterior to the larger carried a posterior palatine branch of the 7th nerve. A lateral head vein canal has not been seen in *Gillicus*. Because the neurocrania of *Xiphactinus* and *Gillicus* are similar in structure, however, its presence is suspected. The canal could easily be crushed on the thin-boned *Gillicus* neurocrania. Foramina entering the postorbital wall and roof of the myodome (KU nos. 965, 11676, 10321) correspond to those of *Xiphactinus*.

The two pterosphenoid foramina for secondary branches of the superficial ophthalmic nerves lie farther anterolaterally (KU nos. 480, 11676) than in *Xiphactinus*. A transverse plate of the basisphenoid spans the anterior opening of the endocranial cavity. The ventral process of the basisphenoid extends less than halfway to the parasphenoid.

A narrow longitudinal depression deeply incised in the basioccipital distinguishes the lateral surface of this bone. In lateral view a piece of the exoccipital appears between the intercalar and basioccipital. When the intercalar is removed (KU no. 480) the exoccipital is seen to occupy a large part of the posterolateral neurocranial wall. Foramina in the exoccipital differ in some details from their arrangement in *Xiphactinus*, since two foramina for occipital nerves lie dorsomedial to the depression for osseous brushes (Fig. 19) and only one such opening is seen in *Xiphactinus*. These foramina occur on the exoccipital wing which abuts against the neural arch of the first centrum. The lateral wall and part of the floor of the large canal leading from the rear of the neurocranium into the subtemporal fossa is formed by the intercalar. In *Xiphactinus* this canal is surrounded entirely by the exoccipital. The lateral head vein passed through this canal to enter the subtemporal fossa. Separate foramina for the 9th and 10th nerves appear on the medial surface of the exoccipital (KU no. 11679). Pathways of these nerves converge within the exoccipital and a single foramen carried both nerves to the posteromedial end of the large canal. The supratemporal branch of the 9th nerve separated from the branchial branch of the nerve and emerged from the dorsomedial corner of the large canal.

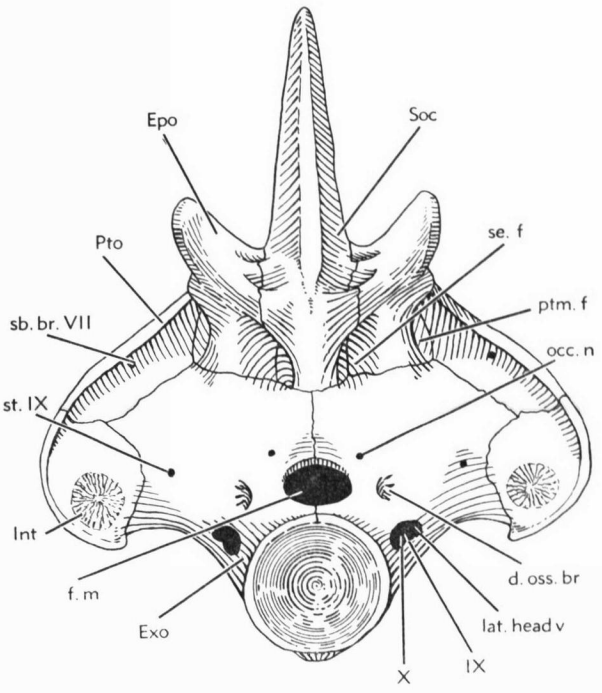

FIGURE 19. *Gillicus arcuatus* (COPE). Restoration of posterior aspect of neurocranium (based on KU Nos. 965, 11679), ×1. [For explanation of abbreviations see p. 4.]

The intercalar forms approximately one-quarter of the hyomandibular fossa. The posterior protuberance for the intercalar arm of the post-temporal is characterized by an irregularly crinkled surface.

Two large round sclerotics surround the perimeter of the eye. There is no evidence of a posterior osseous cup.

[*Maxillary-mandibular bones.*] *Gillicus* premaxillaries have been described previously only in the English Chalk species *G. serridens* WOODWARD (1901). These small thin bones, easily separated from the maxillary, are not commonly preserved. The alveolar border of preserved specimens is frequently incomplete. The premaxillary is approximately rhomboidal in profile. The ventral border is straight, whereas the dorsal and posterior margins have irregularly wavy edges. The anterior border rises vertically then curves posterodorsally (Fig. 20,*A*). Mean number of

EXPLANATION OF PLATE 2

GILLICUS, PROPORTHEUS

FIGURE

A. Gillicus serridens (WOODWARD). Holotype. BMNH no. P.8633, approx. X1. (Photograph courtesy of Dr. E. I. White, BMNH.)

B. Proportheus kameruni JAEKEL. AMNH no. 6302, approx. ×0.25. (Photograph courtesy of Dr. B. Schaeffer, AMNH.)

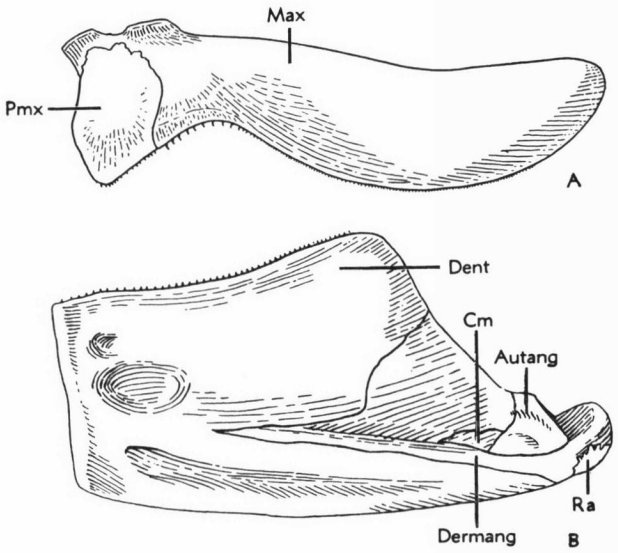

FIGURE 20. *Gillicus arcuatus* (COPE).——*A*. Lateral view of premaxillary and maxillary (KU no. 11680), ×0.75. ——*B*. Internal view of mandible (KU no. 136), ×0.75. [For explanation of abbreviations see p. 4.]

premaxillary alveoli is 13.6 (10-17 in 9 specimens). As in *Xiphactinus* and *Ichthyodectes,* the alveolar border length and ratio of alveolar border length to diagonal height increase in premaxillaries with a larger number of alveoli. Asymmetry in number of alveoli in right and left premaxillaries of any individual probably occurs in *Gillicus* but pairs of premaxillaries are uncommon. One specimen (KU no. 738) has 15 left and ?13 right premaxillary alveoli. Teeth in anterior alveoli are anteroposteriorly compressed and approximately 1.5 mm. in transverse diameter and 1 mm. in anteroposterior length. Posterior teeth are round.

The saber-shaped maxillary (Fig. 20,*A*) distinguishes *Gillicus*. The posterior end of this bone lies below the middle of the orbit. The anterior or ethmoid condyle is approximately circular and extends onto the medial surface of the maxillary. The medial extension of the anterior condyle abuts on the lateral articular facet of the vomer. The posterior, ellipsoidal maxillary condyle does not show the irregular marginal embayments characteristic of *Xiphactinus*. In profile, the dorsal maxillary margin is concave behind the posterior condyle. A paraboloid notch, approximately 1 cm. deep, developed at the start of the alveolar border characterizes the ventral profile. Posterior to this notch the dental border forms a saber-like curve, which is more strongly convex than the dorsal border is concave. The maxillary is approximately uniform in thickness throughout its length. The lower half of its external surface has numerous small pits which open into shallow grooves extending posteriorly.

Mean length of the maxillary alveolar border is 7.6 cm. (range 7.2-11 cm. in 19 specimens; standard deviation 1.4 cm.). Mean height of maxillary at posterior condyle is 2.3 cm. (range 1.1-3.2 cm. in 21 specimens; standard deviation 0.14 cm.). Teeth are preserved only in the paraboloid notch of the alveolar border. They are conical in shape, 1 mm. high, and curve posteromedially. Approximately 150 alveoli appear on the saber-shaped part of the alveolar border. Crowns of minute teeth which barely project above the alveolar border appear in the alveoli. Two supramaxillaries (KU no. 129), proportionally higher and shorter than in *Xiphactinus*, cover the ventrolateral section of the cheek.

The mandible consists of 5 bones—dentary, dermangular, autangular, retroarticular, and coronomeckelian (Fig. 20,*B*). The dentary alone is most commonly preserved. In profile the alveolar border rises slightly behind the symphysis. Within approximately 1 cm. the border forms a gently concave curve which rises gradually to the coronoid process. A narrow anteroposterior ridge on the medial surface of the mandible is formed by the dermangular posteriorly and the dentary anteriorly. The anterior end of this ridge curves gently upward into the symphysis. Just above the anterior end of the ridge an oval depression with diameter approximately one-half of the symphysis length is incised in the dentary. Hypohyals lay in this depression. Five pits for receptor organs of the mandibular sensory canal occur just above the posteroventral margin of the dentary. The quadrate-mandibular articular facet, formed entirely by the autangular, lies proportionally closer to posterior end of the alveolar margin in *Gillicus* than in *Xiphactinus* or *Ichthyodectes*.

Mean length of the mandible is 10.4 cm. (range 7.7-11.9 cm. in 7 specimens; standard deviation 1.5 cm.). Mean length of the symphysis is 3.7 cm. (range 2.5-4.8 cm. in 24 specimens; standard deviation 0.6 cm.). A mean angle of 103 degrees (range 100-107 degrees in 9 specimens; standard deviation 2.7 degrees) is formed between anterior and ventral margins of the mandible. Mean length of the alveolar border is 5.6 cm. (range 1.9-7.5 cm. in 11 specimens; standard deviation 1.5 cm.). The dentary with a 1.9 cm. long alveolar border is the smallest *Gillicus* lower jaw known. The next smallest specimen measures 4.6 cm. along the alveolar border.

Pieces of the alveolar border are missing on most dentaries. A complete one (KU no. 136) has 65 alveoli. Alveolar counts of incomplete dental margins on other specimens approach this number. Mandibular teeth are approximately 0.5-1 mm. in height, laterally compressed, and inclined posteriorly. Tips of the teeth curve medially. Numerous irregular notches and indentations occur on the medial margin of the alveolar border.

[*Hyopalatine bones.*] The thin hyomandibular is bent sharply forward below the neurocranial articulation so that the mandibulo-quadrate articulation lies beneath the middle of the orbit. The opercular head is narrow dorsally and expanded ventrally. A single, elongate ellipsoidal depression lies in front of the opercular head. A thin ridge runs anterodorsally across the medial surface of the hyomandibular from the ventral end of the opercular head to the anterior end of the neurocranial head. Only incomplete mesopterygoids and metapterygoids are preserved. The mesopterygoid and metapterygoid form a groove for the basipterygoid process. The ectopterygoid (KU no. 135) is

proportionally shorter and more sharply angled than in *Xiphactinus* and *Ichthyodectes*. Mean ratio of palatine malleolar height to length is 53.

The articular facet of the mandibular head of the quadrate is directed ventrally, rather than twisted anteroventrally as in *Xiphactinus*. The narrow elongate head has parallel borders without embayments as in *Xiphactinus*. The narrow cleft in which the symplectic lies extends more than halfway to the base of the quadrate.

[*Circumorbital bones.*] These bones are not well preserved and only the pair of nasals can be described. The hind end of the posterior, narrow, elongate nasal (KU no. 11675) is inserted into a notch in the frontal above the dorsoposterior margin of the nasal capsule. A line of 4 small pits for sense organs of the supraorbital sensory canal appears on the dorsal surface of this bone. The anterior nasal is wider and flatter and covers the middle and anterior part of the nasal capsule. Seven pits for supraorbital sensory canal sense organs occur on the dorsal surface.

[*Opercular bones.*] The lower half of the preoperculum is a broad thin plate with a straight ventral border. The posteroventral corner forms a right angle (USNM no. 21081). A narrow dorsal process of the preoperculum extends between the articular head of the operculum and vertical ridge of the hyomandibular. A line of 12-14 pits of the preopercular sensory canal open ventrolaterally from the platelike part of the preoperculum. Shallow grooves extend ventroposteriorly from these pits.

The opercular profile is more sharply rounded dorsally, ventrally, and posteriorly than in *Xiphactinus* and *Ichthyodectes*. The anterior border slants posteroventrally (KU nos. 135, 146) from the mandibular articulation rather than vertically. The lateral opercular surface is marked by fine lines which extend posteriorly and posteroventrally from the articular head. Preserved parts of the interoperculum (KU nos. 129, 135) indicate that the bone is strengthened by a longitudinal ridge and its surface is marked with irregular tubercles.

[*Hyobranchial bones.*] The ceratohyal is proportionally shorter and thicker than in *Xiphactinus*. Least ceratohyal width (KU no. 135) is contained approximately 2.5 times in its length. The epihyal is less than one-third the length of the ceratohyal. The interhyal (KU no. 129) is a short, rod-shaped bone rounded dorsally and flattened ventrally. Branchiostegals are not preserved.

Ceratobranchials are elongate, flattened bones. The first is 2-3 times wider than succeeding ones. A flat, thin, isolated pharyingobranchial, approximately 1 cm. in length (KU no. 10321), is characterized by a mid-longitudinal transverse twist. Compressed, dagger-like gill rakers have bladelike edges. Such rakers appear on the 1st and 2nd ceratobranchials. The gill rakers are flatter and longer than the spikelike rakers of *Ichthyodectes*. Some of them, covered by minute teeth, exceed 4 cm. in length.

[*Vertebrae and ribs.*] The vertebral column forms a straight line. One with 69 centra (FH no. 5026) shows 42 abdominal and 27 caudal. Incomplete columns definitely assignable to *Gillicus* respectively have centra counts of 57 (KU no. 146), 52 (KU no. 11679), and 49 (KU no. 10274). Anterior abdominal centra are smaller than those

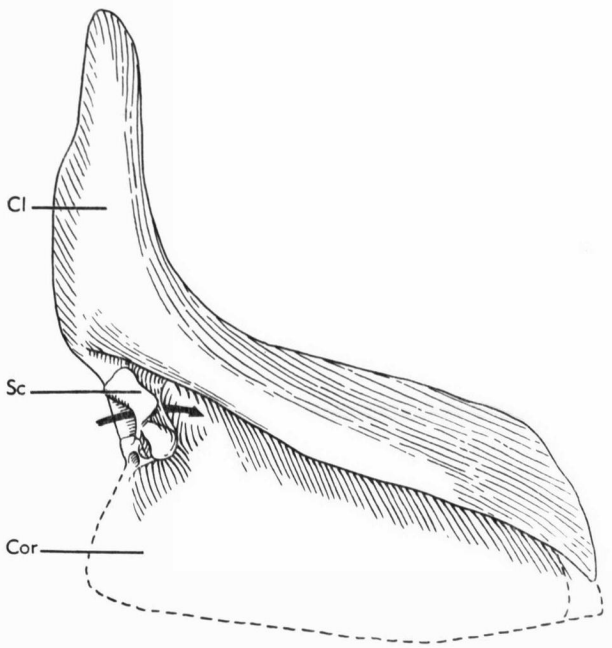

FIGURE 21. *Gillicus arcuatus* (COPE). External view of pectoral girdle (KU No. 346), ×0.75. [For explanation of abbreviations see p. 4.]

of *Ichthyodectes*. However, mid-trunk and anterior caudal centra may attain dimensions approximately equal to those of *Ichthyodectes*. The first centrum (KU no. 146) measures 1 cm. in length and 1.6 cm. in height and width. Mid-abdominal centra (KU no. 10321, AMNH no. 8178) are about 2 cm. long and 3 cm. in height and width.

Shape and proportions of centra ridges and grooves are identical to those of *Ichthyodectes*. Lateral grooves and ridges appear initially on the 2nd and are well defined on the 3rd centrum (KU nos. 146, 478, 11679). The grooves and ridges disappear by the 6th from last centrum. Dorsal pits for neural arches occur on all centra. Pits for hemal arches are lacking on anterior centra but appear on posterior ones. The exact point of origin of hemal arches cannot be determined. Each centrum except the first is penetrated by the notochord.

The caudal fin support involves 6 centra, the last 4 of which are turned slightly upward. Hemal arches of the 5 centra anterior to the terminal centrum are expanded proximally. These help to stabilize the caudal fin. The neural and hemal arches are firmly united to the centra. Structure of hypurals (KU no. 10274) is similar to that of *Xiphactinus*.

Each of the anterior neural arches joins the arch anterior and posterior to it. Epineural ribs arise from the bases of the arches. Depressions for insertion of epipleural ribs (KU nos. 146, 10274) appear near the anterior end of the longitudinal lateral ridge of abdominal centra but the number of them with depressions cannot be determined. Pleural ribs are inserted by parapophyses anteriorly. The parapophyses occupy the lower of the 2 lateral grooves be-

ginning with the 3rd centrum. Pleural ribs are attached to hemal arches posteriorly.

[*Pectoral and pelvic girdles.*] Post-temporal, extrascapular, and supracleithrum are not preserved. In lateral view (Fig. 21) the vertical arm of the cleithrum (KU nos. 135, 146, 346) does not extend to the level of the vertebral column and its horizontal arm is proportionally larger than in *Xiphactinus*.

Articular facets of the scapula lie approximately parallel to the vertical body axis but incline posteriorly at about 45 degrees to the horizontal axis. The uppermost of the 3 scapular facets is ovoid and gently convex. The lower 2 facets are conjoined and respectively concave and convex.

The proximal surface of the first flattened actinost has a single articular facet which is dorsoventrally enlarged and articulated with the 2 conjoined lower facets of the scapula. The distal surface of the first actinost bears 2 separate ventral facets and a single dorsolateral one. The 2nd and 3rd actinosts are T-shaped.

The posterior end of a pelvic girdle (KU no. 66) is tentatively referred to *Gillicus*. This specimen is not associated with other skeletal parts of the genus. Articular facets on each side of the fused basipterygia are continuous posterolaterally rather than separated into dorsal and ventral entities.

[*Fins.*] Dorsal and anal fins are not preserved. The caudal fin is deeply cleft. It has 10 dorsal and 9 ventral principal rays, which are segmented transversely in a zigzag pattern. Longitudinal division and segmentation of rays of the dorsal lobe occur more proximally than on the lower lobe.

A complete pectoral fin is not preserved. There are 8 or 9 pectoral fin rays on KU no. 143. All rays are longitudinally but not transversely divided distally. Longitudinal division of the first ray involves only its posterior half. Width of the first ray is 1.25 times that of the second ray.

[*Scales.*] Mid-body ellipsoidal scales reach 4.5 cm. in height and 3 cm. in length (Fig. 13,*D*). Twenty to 30 short, discontinuous, and deeply incised anterior radii are present. They do not reach the scale nucleus. A broad posterior part of the scale is marked with dense, minute punctae which become larger and less closely spaced toward the scale nucleus. The punctae are arranged in rows. Toward the middle sector of the scale the rows of punctae are especially distinct. Scales lying just behind the head are round (Fig. 13,*C*) and approximately 3 cm. long and 3 cm. high. Punctae of these scales are finer. A canal for the lateral line traverses the posterior half of some mid-body scales.

Discussion. Hay distinguished *Gillicus* from *Ichthyodectes* by a smaller gape and relatively greater depth of the mandible in relation to its length. Taxonomic history of *G. arcuatus* and *G. polymicrodus* was traced by Hay (1898b). Three species are now added to the synonymy of *G. arcuatus*. *I. acanthicus* Cope (holotype, AMNH no. 2091) consists of a parasphenoid, fragment of dentary alveolar border, and a worn vertebral fragment which may not belong to the same fish as the other material. The narrow, quadrilateral parasphenoid resembles that of *Gillicus*. The thin alveolar fragment with 3 slender medially curved teeth located in alveoli perhaps belongs to *Gillicus* but the teeth are larger than those of *Gillicus* and the jaw fragment may belong to *Pachyrhizodus*. *G. arcuatus* was placed in synonymy with *I. occidentalis* (Leidy), a new name combination of Loomis (1900). The holotype of *I. occidentalis* is a scale that probably belongs to *Ichthyodectes* (see discussion of *I. ctenodon*). All material described and figured by Loomis (pl. 23, figs. 1-6) belongs to *G. arcuatus*. Cockerell (1919) named a scale from KU no. 143 as *Hypsodon audax*. He did not study other parts of this fossil which include neurocranium and jaws clearly pertaining to *G. arcuatus*.

Several isolated scales which may belong to *Gillicus* have been named. Cockerell (1919, pl. 32, fig. 5) applied the name *Hypsodon? granulosus* to a scale bearing numerous posterior punctae and less than a dozen short anterior radii. This scale (USNM no. 8678), from the Mowry Shale near North Rawlins, Wyoming, is similar to round anteroventral abdominal scales on KU no. 143, except that the radii are not as well developed. If actually a *Gillicus*, this scale is the earliest record of the genus in North America. The name *Hypsodon lowii* (Cockerell) was established for a scale (Cockerell, 1919, pl. 34, fig. 2) which tapers dorsally and ventrally. Anterior radii are elongate and discontinuous. Fine posterior punctae are developed as on other scales which are associated with neurocrania or jaws referable to *Gillicus*. This specimen (USNM no. 8683), from the "Benton Formation" of North Park, Colorado (sec. 20, T. 9 N., R. 77 W.), is assignable to *Gillicus*. Scales referred to *Cladocyclus occidentalis* by Whiteaves (1889), Tyrrell (1892) and Lambe (1905) show the same structure as those of KU no. 143. The scales come from several Vermilion River Formation sites in Manitoba, Canada.

Dr. Sloan has shown me isolated scales which I believe belong to *Gillicus*. They are from the Carlile Shale (SW¼, sec. 18, T. 120 N., R. 47 W.) in Grant County, South Dakota. He has also shown me a pectoral fin of *Gillicus* from the Niobrara Formation of Lac Qui Parle County, Minnesota (NE¼, SW¼, sec. 15, T. 120 N., R. 45 W.). This fin is referred to *Gillicus* because the posterior half of the first ray is divided longitudinally as in other *Gillicus* pectoral fins from the Niobrara Formation of Kansas.

GILLICUS SERRIDENS (Woodward), 1901

Plate 2, figure *A*

Ichthyodectes serridens Woodward, 1901, p. 101, pl. 8.
Gillicus serridens Hay, 1903a, p. 59.

Holotype. Head and anterior vertebrae (BMNH No. P. 8633). Albian, Folkestone, Kent, England.

Geologic occurrence and distribution. Only the holotype is known.

Diagnosis. Mouth cleft opens anteriorly. Orbit shorter than snout.

Discussion. This species is tentatively considered distinct from *Gillicus arcuatus*, primarily for reasons of its geographic and geologic position. *G. serridens* cannot be distinguished from *G. arcuatus* by larger anterior mandibular teeth or a more slender maxillary as Woodward (1901) suggested. These are also features of *G. arcuatus*.

Genus CHIROCENTRUS Cuvier, 1817

Chirocentrus Cuvier, 1817, p. 178.
Jeosudis Castelnau, 1873, p. 118.

Type-species. Clupea dorab FORSKÅL, 1775, p. 7.
Geologic occurrence and distribution. Recent, East African coast from Natal to Red Sea; eastward to India, Malaya, New Guinea and Queensland; north to Philippines, Taiwan, China and Japan.

Diagnosis. Elongate, laterally compressed fishes attaining a standard length of approximately 1 m. Abdomen trenchant, lacking scutes. Maximum depth of trunk contained 5-8 times in standard length. Head contained 5-6 times in standard length. Maximum depth of head included 1.3-1.7 times in head length. Height of caudal peduncle contained 2.3-3.0 in its length. Supraoccipital crest low, exceeded in height by parietoepiotic crest. Contact of supraoccipital and frontals separates small parietals. Temporal foramen and preepiotic fossa present. Basisphenoid without vertical arm. Parasphenoid projects posteriorly under first 2-3 anterior centra. Gape of mouth directed upward. Premaxillary with one or two enlarged, ventroanteriorly directed caniniform teeth followed by several smaller conical teeth. Conical maxillary teeth diminish in length posteriorly. Premaxillary and maxillary teeth in shallow alveoli. Mandible with 4-6 large teeth, largest attains 1 cm. in crown height. Mandibular teeth in shallow alveoli and partly fused to alveolar border.

Vertebrae 70-74; 39-46 abdominal, 26-32 caudal. Centra higher than long. Longitudinal lateral ridge between deep depressions. Dorsal fin with 4 undivided and 12-13 divided rays begins over anal fin. Anal fin composed of 1-4 undivided rays and 27-32 divided rays. Pectoral fin with 1 spinose undivided and 12-14 divided rays. Pelvic fin with 1 undivided and 5-6 divided rays. Pelvic fin situated at start of last 3rd of distance between pectoral fin base and anal fin. Thin, deciduous cycloid scales less than 2-4 mm. in height with circuli only.

CHIROCENTRUS DORAB (Forskål), 1775
Text-figures 13,*G*, 22-27

See FOWLER, (1941) for extensive synonymy prior to 1941.
Chirocentrus dorab SMITH, 1950, p. 87, pl. 5.
Holotype. Probably in Paris, Musée National d'Histoire Naturelle.
Geologic occurrence and distribution. Recent, Natal, South Africa, Zanzibar, Mozambique, Mauritius, Red Sea, Persian Gulf, India, Malay peninsula, Thailand, Indonesia, Philippines, China, Taiwan, Japan, Queensland, New South Wales (FOWLER, 1941).

Diagnosis. (Based on HARDENBERG, 1930, and FOWLER, 1941). Elongate, shallow-bodied fishes. Maximum depth of trunk contained a little more than 7 times (range 5.6-8.1) in standard length. Head contained approximately 5.75 times (range 5.3-6.4) in standard length. Maximum depth of head contained about 1.75 times in length of head. Snout contained 3.7-4.25 in head. Diameter of orbit contained 4-4.7 in head and 1-1.7 in snout. Posterior end of maxillary does not reach operculum. Gill rakers 3+14-15. Vertebrae approximately 74; 44 (range 42-46) abdominal and 29-30 (range 28-32) caudal. Dorsal fin IV, 13. Anal fin I—IV+27-32. Pectoral fin I, 13 (range 12-14). Pelvic fin I, 6.

Description. The anatomy of *Chirocentrus dorab*, with special emphasis on soft structures, was first described by CUVIER & VALENCIENNES (1846). RIDEWOOD (1904b) provided an account of the head structure but did not describe the neurocranium in detail. STARKS (1930) described the pectoral girdle and JACOBSHAGEN (1937) reported on structure of the spiral valve.

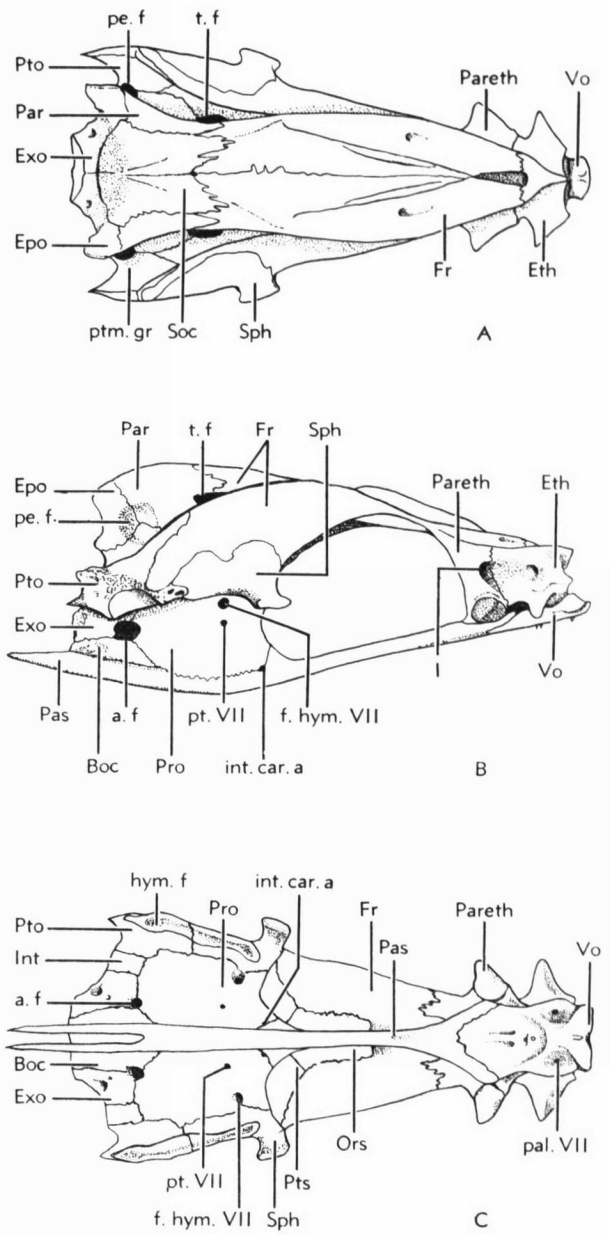

FIGURE 22. *Chirocentrus dorab* (FORSKÅL).——*A*. Dorsal view of neurocranium.——*B*. Lateral view of neurocranium.——*C*. Ventral view of neurocranium. All ×3. [For explanation of abbreviations see p. 4.]

[*Body form.*] *Chirocentrus dorab* is a long, narrow-bodied fish. Specimens attain a length of approximately 1 m. (HARDENBERG, 1930), not 4 m. as SMITH (1950), following CUVIER & VALENCIENNES (1846), stated. The statement of these authors concerning size, was based on reports of fish peddlers and not on actual specimens. In

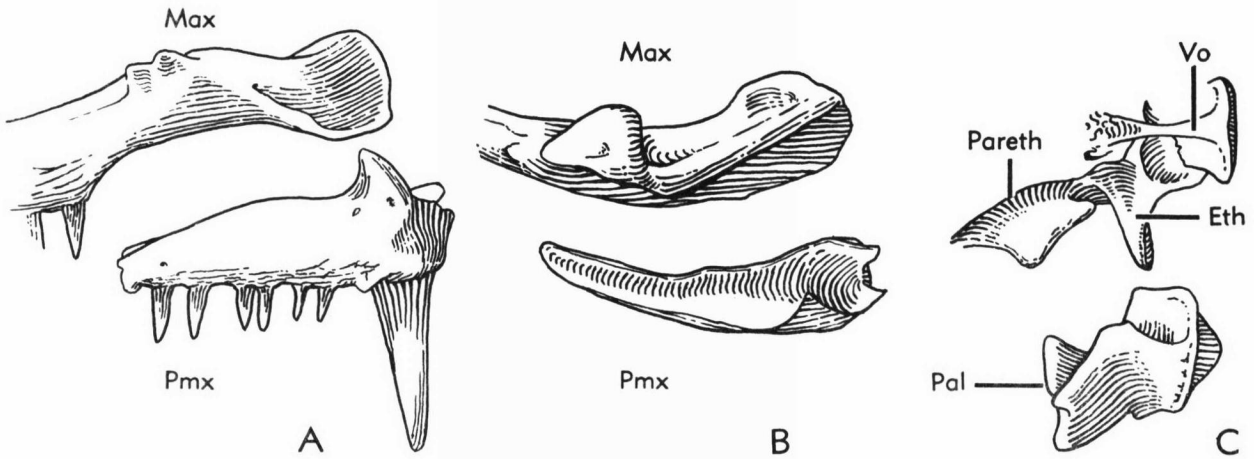

FIGURE 23. *Chirocentrus dorab* (FORSKÅL). Articulations between premaxillary and maxillary; palatine and snout. ——*A*. Lateral view of premaxillary and anterior end of maxillary.——*B*. Dorsal view of premaxillary showing groove for anterior end of maxillary.——*C*. Dorsal view of palatine and anterior end of neurocranium. All ×3. [For explanation of abbreviations see p. 4.]

transverse section the dorsal margin is gently rounded. Sides of the body taper to a sharp ventral edge which has no scutes.

[*Neurocranium*.] In dorsal view (Fig. 22,*A*) the wedge-shaped neurocranium tapers anteriorly. Arms of the parethmoid and ethmoid project laterally. Two crests originating dorsal to the orbit diverge and extend posteriorly and ventroposteriorly. The posteriorly directed ridge is composed of frontal, parietal, and epiotic. The ventroposteriorly directed ridge is formed by frontal and pterotic. In this paper, the ridges are referred to as medial and lateral, respectively. The elongate depression between the ridges is the post-temporal groove. A stout sphenotic process projects from the lateral margin of the neurocranium.

In lateral view (Fig. 22,*B*) the greatest neurocranial height occurs at the level of the trigeminofacial chamber. The orbit and snout become narrow as the parasphenoid angles dorsoanteriorly across the orbit. The postorbital section of the neurocranium lies in a plane parallel to the long axis of the body.

The vomer is the most anterior element of the neurocranium. Its anterior end curves gently upward, lateral margins of the anterior process being dorsoventrally concave (Fig. 22,*C*). The anterior end of the maxillary abuts against the concave surface. The vomer broadens posteriorly and the ventral surface becomes slightly concave. Three teeth occur along the ventral vomerine surface. Such teeth were not seen by RIDEWOOD (1904b). One tooth is located on the anterior process; the other 2 are found, one behind the other, at the anterior end of the concave surface. Two foramina appear on ventral vomerine surface at level of the lateral ethmoid process. The palatine ramus of the 7th nerve emerges through these foramina.

The ethmoid has a bladelike vertical anterior projection and a lateral projection also (Fig. 23,*C*) that fits snugly into an anterior pocket on dorsomedial surface of the palatine. This lateral process is concave anteriorly and continuous with the dorsoventrally concave surface of the vomer. The anterior condyle of the maxillary in part abuts on this surface of the ethmoid. The dorsal surface of the ethmoid is covered with fine punctae. A foramen anterior to nasal capsule on lateral side of the ethmoid is continuous with the palatine foramen of the vomer.

The parethmoid joins the frontal dorsally, the ethmoid anteriorly, and the parasphenoid ventrally. A lateral projection of the parethmoid fits into a posterior pocket on the dorsomedial surface of the palatine (Fig. 23,*C*). Parethmoids meet at the mid-sagittal line in an interdigitating suture so as to form the anterior wall of the orbit. A foramen in each parethmoid just lateral to the mid-line carries the olfactory nerve into the nasal cavity, which lies above the anterolaterally expanded palatine head of the parethmoid and lateral process of ethmoid. The parethmoid palatine head is convex on its articular surface, which is directed ventrally. Endochondral and dermal elements of the parethmoid cannot be distinguished.

Frontals are elongate narrow bones which meet the ethmoid anteriorly, the supraoccipital, parietals, and pterotics posteriorly, and the sphenotics posterolaterally. A flange of the frontal extends posteroventrally across the lateral surface of the pterotic. This flange ends just below the hyomandibular fossa and posterior to a foramen in the pterotic for the preopercular-mandibular sensory canal. A median elongate fontanelle lies between anteromedial ends of the frontals posterior to the ethmoid. The frontals form a concave depression anteromedial to the supraoccipital-frontal suture. A pinpoint foramen, much smaller than that figured by RIDEWOOD (1940b, fig. 118), is present at the point where 3 bones (supraoccipital, 2 frontals) join at the mid-sagittal line. This foramen is present on only one of the 5 specimens examined. RIDEWOOD saw it on one of his 3 specimens. Anterior halves of lateral and medial ridges are formed by the frontal. Between lateral and medial ridges the frontal produces the anterior part of the post-temporal groove. Frontal and parietal surround the

temporal foramen, which projects directly into the endocranial cavity. The frontoparietal suture extends across the medial surface of the medial ridge and intersects the supraoccipito-frontal suture. Above the orbit, the ventral surface of each frontal exhibits an elongate groove. A pair of foramina through which superficial ophthalmic branches of the 7th nerve pass to supply sensory canals of the head appear in each groove.

The sphenotic is characterized by a stout lateral process. The anterior half of the hyomandibular fossa is incised in the ventrolateral wall of the sphenotic. Part of the posterior orbital wall is formed by the sphenotic. A foramen for the otic branch of the 7th nerve penetrates the orbital face of this bone.

Parietals are separated by the expanded supraoccipital. The middle section of the medial ridge and part of the median wall of the post-temporal groove are produced by the parietal, which joins the pterotic ventrally, the epiotic posteriorly, the frontal anteriorly and ventrally, and the supraoccipital medially. The anterodorsal section of the preepiotic fossa lies within the parietal.

The supraoccipital expands broadly over the posterodorsal neurocranial roof. This bone joins the frontals anteriorly, epiotics posterolaterally, parietals laterally, and exoccipitals posteroventrally. A low supraoccipital crest is developed at the posterodorsal end of the neurocranium. This crest is hidden in profile view by the higher medial ridge.

The epiotic forms the posterior part of the medial ridge and the posteromedial wall of the post-temporal groove. The epiotico-parietal suture runs ventromedially into the preepiotic fossa ending against the pterotic.

The pterotic joins the frontal anterolaterally, epiotic and parietal medially, exoccipital posterolaterally, and intercalar ventrally. The floor of the preepiotic fossa, as well as the posterior floor and posterolateral wall of the post-temporal groove is formed by the pterotic. The posterior section of the hyomandibular fossa is engraved in the pterotic. Part of the pterotic below the hyomandibular fossa contributes to the lateral neurocranial wall. Two short spines extend rearward from the posterolateral corner of the pterotic. A single foramen opens posteriorly from pterotic at the base of these spines. A pair of foramina open laterally from the pterotic below the posterolateral flange of the frontal. The 3 foramina are apertures for sensory canals. Indentations in the posterior surface of the pterotic indicate points of attachment of epaxial muscles (Fig. 24,*A*).

The parasphenoid is concave under the anterior end of the orbit and triangular in cross section below the middle of the orbit. The floor of the myodome canal is formed by the parasphenoid. An ascending process of this bone produces the anterior walls of the myodome canal. A foramen for the internal carotid artery passes through the ascending process just below the juncture of the ascending process of the parasphenoid and prootic. A foramen for an efferent pseudobranchial artery is absent in *Chirocentrus* in correlation with the absence of a pseudobranch. Below the auditory fenestra the parasphenoid divides into a pair of processes which extend posteriorly under the first 2 or 3 centra.

The prootic is the largest bone on the lateral surface of the neurocranium. It forms the anterior two-thirds of the lateral neurocranial wall and part of the postorbital wall. On the lateral wall the prootic joins the intercalar, basioccipital, and exoccipital posteriorly and forms the anterior wall of the auditory fenestra. In orbital view the prootic contacts pterosphenoid dorsomedially and sphenotic dorsolaterally. Prootic and pterosphenoid surround

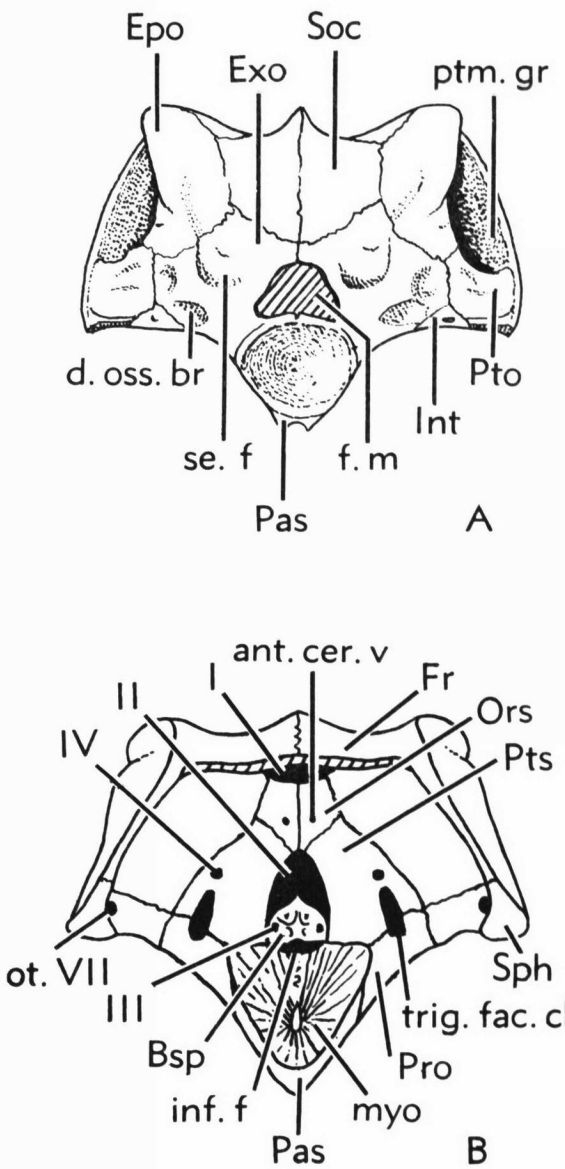

FIGURE 24. *Chirocentrus dorab* (FORSKÅL).——*A*. Posterior view of neurocranium.——*B*. Postorbital neurocranium wall. Both ×3. [For explanation of abbreviations see p. 4.]

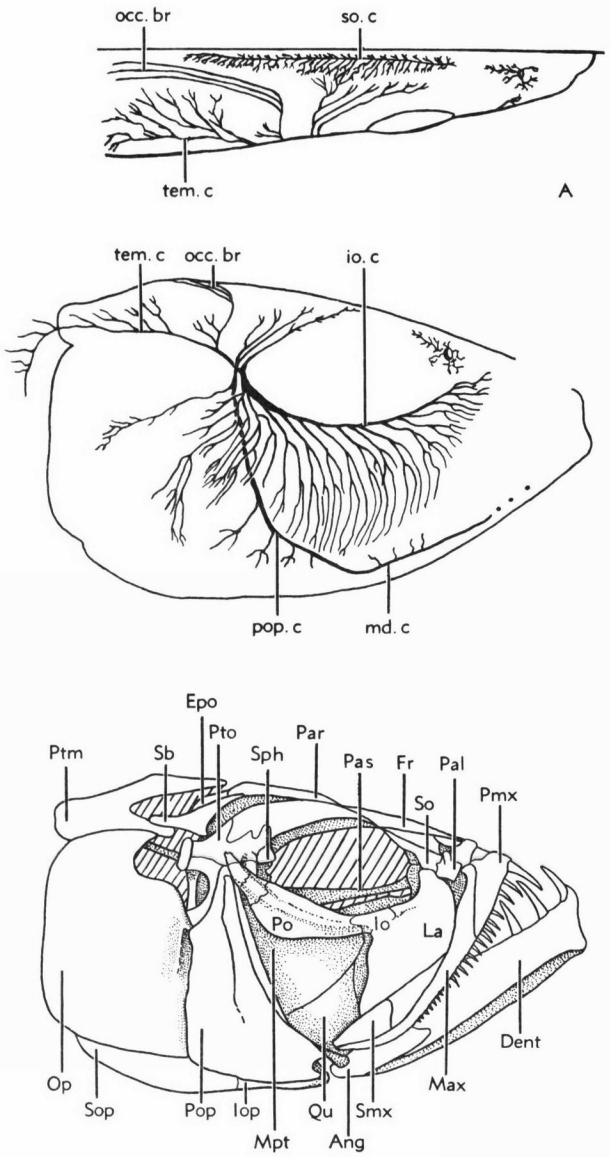

FIGURE 25. *Chirocentrus dorab* (FORSKÅL).——*A*. Dorsal view of cephalic sensory canals.——*B*. Lateral view of cephalic sensory canals.——*C*. Lateral view of head. All ×1. [For explanation of abbreviations see p. 4.]

the trigeminofacial chamber. Medially directed processes of each prootic meet to produce the roof of the myodome canal.

A bulge on the lateral surface of the prootic just behind the trigeminofacial chamber marks the site of the anterior osseous capsule, which contains a diverticulum of the swim bladder. The posterior osseous capsule is indicated by a less conspicuous bulge in the pterotic below the preepiotic fossa. A 2nd diverticulum of the swim bladder lies in this capsule. [See BEAUFORT (1909) and SRIVASTAVA (1956) for a description of the swim bladder in *Chirocentrus*.] The auditory fenestra, bordered by prootic, basioccipital, and exoccipital is covered by a thin membrane. An anterior projection from the swim bladder lies snugly against this membrane.

Two foramina open from the lateral surface of the prootic, the lower one comprising the exit for the pretrematic branch of the 7th nerve. The hyomandibular branch of the 7th nerve passes through the upper opening. No canal for the lateral head vein appears in *Chirocentrus*. This vein enters the upper of the 2 foramina and emerges from the trigeminofacial chamber into the orbital cavity.

The pterosphenoid forms the anterior end of the endocranial cavity. This bone meets the basisphenoid medially, orbitosphenoid anterodorsally, frontal laterally, prootic ventrally, and sphenotic ventrolaterally. Pterosphenoid, basisphenoid and orbitosphenoid surround the optic foramen.

The trigeminofacial foramen is the largest opening on the posterior wall of the orbit (Fig. 24,*B*). Mandibulomaxillary branches of the 5th nerve, the buccal branch of the 7th nerve, superficial ophthalmic branches of the 5th and 7th nerves and the profundus branch of the 5th nerve emerge together through the trigeminofacial foramen. The otic branch of the 7th nerve also emerges from this opening and extends dorsolaterally along the postorbital wall to enter a foramen in the sphenotic. Within the sphenotic this nerve joins the recurrent branch of the 7th nerve and passes posteriorly into the lateral recess of the skull. The trochlear nerve enters the orbital cavity through the trigeminofacial foramen in three of the five specimens examined. Two specimens exhibit a small foramen which is entirely enclosed by the pterosphenoid and lies dorsal to the trigeminofacial foramen. In these two individuals the trochlear nerve emerges from the endocranial cavity through this foramen. The palatine branches of the 7th and the 6th nerves enter the myodome canal through the prootic roof of this canal at level of the anterior osseous capsule.

The single orbitosphenoid extends anteriorly from the pterosphenoids. Laterally the orbitosphenoid meets each frontal and posteriorly forms the dorsoanterior margin of the optic foramen. A thin orbitosphenoid projection extends anteriorly toward the parethmoid but does not reach the latter. Olfactory nerves lie in a space above the orbitosphenoid and below the frontals. A foramen for the anterocerebral vein penetrates each side of orbitosphenoid posteromedially.

The small basisphenoid lacks a vertical process dividing the myodome canal. This bone forms the anteroventral boundary of the endocranial cavity. Basisphenoid and prootic surround the median ventral infundibular foramen. Foramina for the oculomotor nerve pierce each side of the basisphenoid near juncture of this bone and the pterosphenoid. External rectus muscles are attached to a pair of excavations on either side of the basisphenoid midline.

The anterior half of a centrum is fused with the basioccipital at the posteroventral end of the neurocranium. Medial wings of the basioccipital roof the myodome canal posteriorly and form the posterior floor of the saccular re-

cess. The ventral margin of the auditory fenestra is rimmed by the basioccipital.

The exoccipital meets the basioccipital ventrally, the intercalar dorsolaterally, the pterotic posterolaterally, the epiotic dorsally, the supraoccipital dorsomedially, and the prootic anteriorly. Exoccipitals of each side meet to form roof and floor of the foramen magnum (Fig. 24,*A*). Several depressions appear on the posterior surface of the exoccipital. The lateral and lower of these depressions lodge the osseous brushes. The dorsomedial depression forms the subepiotic fossa. Ninth and 10th nerves emerge together through an opening in the lateral face of the exoccipital. A separate opening for the 9th nerve occurs within the endocranial cavity but as one traces the pathway of this nerve laterally it enters the vagus canal.

The small intercalar joins the prootic anteriorly, the pterotic dorsally, the exoccipital ventrally and dorsomedially. A small section of the lateral neurocranial wall is formed by the intercalar. A low protuberance on the posterior face of the intercalar receives the intercalar limb of the post-temporal bone.

A pair of thin, semicircular sclerotic bones surround the eye.

[*Maxillary-mandibular bones.*] The premaxillary is 2½ times longer than high. The ventral border is straight. The dorsal border is characterized anterolaterally by a vertical process. A ligament runs from this process to the ethmoid. Behind this process the dorsal border slants posteroventrally. Anteriorly the premaxillary is rounded. Connective tissue only joins the anterior borders of each premaxillary. An elongate concave groove on the dorsal surface supports the anteroventral end of the maxillary (Fig. 23,*A,B*).

One or two enlarged, caniniform teeth are present at the front of the premaxillary dental border. This tooth, less than 1 cm. in crown height, points ventroanteriorly. Seven to 9 smaller, conical teeth line the dental margin behind the large tooth. These teeth are lodged in shallow sockets.

The maxillary is a slender, saber-shaped bone which ends posteriorly below middle of the orbit (Fig. 25,*C*). The anterior end angles dorsomedially to meet the vomero-ethmoid facet. Two condylar heads with a depression between them appear on the dorsal surface of the anterior end of the maxillary. The anterior head meets the concave area formed by vomer and ethmoid. A short lateral flange of the palatine fits across the depression. The posterior head abuts on the flat ventral surface of the enlarged lateral process of the palatine malleolus (Fig. 23c). Twenty to 30 shallow depressions, approximately half of which are occupied by teeth, occur along the dental border from contact with premaxillary to a point at which the maxillary begins to curve dorsoposteriorly. These teeth with medially curved tips reach 3 mm. in crown height anteriorly. The upwardly turned posterior part of the maxillary has about 30 minute teeth each less than 0.5 mm. in crown height. Two approximately triangular supramaxillaries lie in the dorsoposterior, concave section of the maxillary.

The mandible is a stout, essentially quadrilateral unit

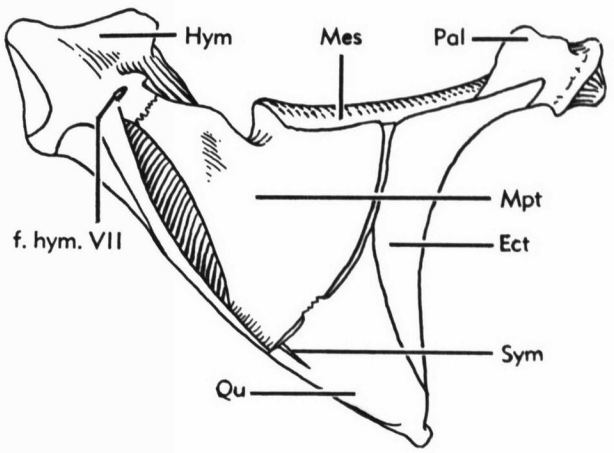

FIGURE 26. *Chirocentrus dorab* (FORSKÅL). External view of hyopalatine bones, ×2. [For explanation of abbreviations see p. 4.]

with the dentary its major element. The dental border is slightly concave anteriorly but rises posteriorly to a low coronoid crest. Behind this crest the dorsal margin of the mandible drops rapidly toward the quadrate-mandibular articulation. The angle between anterior and ventral margins of the dentary is approximately 120°. An elongate, narrow groove on the ventrolateral surface of the dentary carries the mandibular sensory canal. The angular cannot be separated into distinct dermal and endochondral elements but evidence of a suture between these sections is indicated anterior to the quadrate-mandibular articular facet. This facet is concave anteroposteriorly and convex transversely. A slender, elongate retroarticular lies at the ventroposterior end of the mandible. A minute coronomeckelian lies in a groove on the medial side of the mandible anterior to the quadrate-mandibular facet and between anterior extension of angular and dentary. Length of the mandible measured from ventral tip of the symphysis to posterior end of the angular exceeds height of mandible at the coronoid crest by 5-6 times.

Eight to 10 shallow alveoli contain 4-6 teeth (not 8-10 as RIDEWOOD stated). Teeth are ankylosed to alveoli and lateral border of the dentary. The largest tooth reaches approximately 1 cm. in crown height. All teeth are compressed laterally, with sharp anterolateral edges. The teeth curve posteromedially with the tips slightly retroflexed laterally. Replacement teeth of both upper and lower jaws lie suspended in tissue between the emplaced teeth.

[*Hyopalatine bones.*] Below the horizontal neurocranial head the hyomandibular is bent anteriorly in such a way that the lower jaw articulation lies below the middle of the orbit (Fig. 26). The flat medial lamina of the hyomandibular extends as a narrow strut ventrally behind the metapterygoid and medial to the quadrate. A stout, vertical ridge characterizes the lateral hyomandibular surface. This ridge divides dorsally into three parts. One part runs to the anterior, the second to the posterior end of the neurocranial head. Thus, in dorsal view the neurocranial

head is swollen anteriorly and posteriorly and attenuated centrally. The third part runs posteroventrally to the oval opercular head of the hyomandibular. An elongate, thin, lateral lamina of the hyomandibular extends ventrally from that ridge which runs to anterior end of neurocranial head. This lamina joins the metapterygoid ventrally. A part of the levator arcus palatini inserts in the space between lateral and medial laminae of the hyomandibular. A foramen for the hyomandibular branch of the 7th nerve opens from the lateral hyomandibular surface ventroanteriorly to the intersection between the vertical ridge and the ridge which runs to anterior end of the neurocranial head.

The metapterygoid is broadly expanded ventrally. This bone joins the quadrate ventrally along a horizontal line. In two specimens an interdigitating contact of metapterygoid prong and quadrate groove appear midway along the juncture of these bones. An anterior projection of the metapterygoid fits between the ectopterygoid and mesopterygoid. A concave indentation on the dorsomedial edge of metapterygoid anterior to the medial juncture of metapterygoid and hyomandibular may be a remnant of a groove for a basipterygoid process which was present in ancestors of *Chirocentrus*.

The mesopterygoid lies in an essentially horizontal plane. The medial edge of this bone approaches but does not touch the lateral edge of the parasphenoid. Mesopterygoid joins metapterygoid posteroventrally, ectopterygoid ventrally and via a cartilaginous connection meets the palatine anteriorly. No teeth appear on the ventral surface of this bone which forms the roof of the oral chamber.

The boomerang-shaped ectopterygoid extends dorsally from the ventroanterior margin of the quadrate, passes anterior to the metapterygoid and arches anterolaterally along the mesopterygoid. Ectopterygoid and palatine join anteriorly in an interdigitating suture. A small patch of teeth is developed on the anteromedial surface of the ectopterygoid rather than on the palatine as Ridewood stated.

The short, enlarged palatine has several articular facets (Fig. 23,*C*). Dorsomedially an anterior pit recives a lateral prong of the ethmoid. A second pit behind the first is occupied by a lateral process of the parethmoid. An anteroventral protuberance of the palatine fits into a groove behind the posterior head of the maxillary. The posterior maxillary condyle abuts on a flat palatine surface anterior to this protuberance.

The triangular quadrate bears a stout, articular condyle. This condyle is transversely concave and anteroposteriorly convex. A slender, thin elongate symplectic lies in a quadrate cleft which extends ventroanteriorly almost to the articular condyle.

[*Circumorbital bones.*] Eight bones comprise the circumorbital series (Fig. 25,*C*). This series does not completely encircle the orbit. An elongate slender posterior supraorbital lies above the anterodorsal corner of the orbit. This is followed by an anterior supraorbital which is expanded ventrally and covers the posterior part of the parethmoid. The largest circumorbital, the lacrimal, is a plate-like, quadrilateral bone which extends ventrally to the maxillary and posteroventrally to the supramaxillaries. A short, rectangular infraorbital lies in a posterodorsal notch of the lacrimal. Three postorbitals and a minute dermosphenotic complete the circumorbital series. The postorbitals do not reach the preoperculum nor cover the ventroposterior section of the cheek. A short, distally rounded nasal bone lies above the nasal cavity.

Opercular bones. The preoperculum has a stout anterior border; posterior and ventral edges are thin. The horizontal arm is two-thirds the length of the vertical arm. Anterior end of the horizontal arm is notched. The preopercular sensory canal lies in the thickened anterior border of the preoperculum.

The rectangular operculum is approximately 1.3 times higher than wide (Fig. 25,*C*). The stout anterior margin is deeply emarginate near the dorsal border. A cup-shaped articular socket for opercular head of the hyomandibular is situated just below this emargination. The suboperculum tapers in height posteriorly. A process rises dorsally from anterior border of the suboperculum extending upward along anterior end of the operculum. The operculum-suboperculum contact is straight. The ventroposterior margin of the suboperculum is thin. The rectangular interoperculum overlies the anterolateral end of the suboperculum and extends forward medial to the quadrate. At its anterior end the interoperculum is notched where the interopercular-mandibular ligament arises.

[*Hyobranchial bones.*] Ridewood (1904b) described and figured (p. 453) this unit. The lingual plate is covered by coarse, closely spaced, sharp teeth. Structure of gill rakers, especially those on the first ceratobranchial is characteristic of *Chirocentrus*. These rakers were not mentioned by Ridewood. Half of the gill rakers on this arch consist of small, square plaques with 6 to 9 short, sharp, medially directed teeth. Anteroposteriorly compressed, anteriorly projecting rakers alternate with these flat gill rakers. These projecting rakers which taper distally are approximately 3 mm. in length and bear about a dozen medially directed teeth. Such projecting rakers occur only on the upper half of the second ceratobranchial. Teeth of the flat and projecting rakers are finer and more numerous on the second ceratobranchial. Remaining ceratobranchials lack projecting rakers but retain the small, flattened plaques. Ceratohyal and epihyal support 8 branchiostegal rays.

[*Sensory canals.*] Distribution of sensory canals of the head resembles that of *Clupea harengus* (Bamford, 1941). The preopercular-mandibular canal lies in a tube near the anterior border of the preoperculum (Fig. 25,*B*). Two branches extend posteroventrally from this canal across the operculum. The mandibular section of this canal lies in the elongate ventrolateral groove of the dentary. The infraorbital canal, lodged in the lacrimal, infraorbital and postorbital bones, sends numerous branches posteriorly and ventrally. Two dorsal, posteriorly directed branches reach the operculum. Other more ventral branches extend over the preopercular-mandibular canal. Three branches extend from the infraorbital and one from the preopercular canal anterodorsally above the eye. The supraorbital canal runs from the nasal opening to the back of the head (Fig. 25,*A*). Numerous pores open onto the dorsal surface of the head from the supraorbital sensory canal. The temporal sensory

canal arises from the same anterolateral pterotic foramen from which preopercular and infraorbital canals emerge. The temporal sensory canal extends posteriorly to meet the lateral line. A large occipital branch arises from the temporal canal. This branch extends dorsally and divides on top of the head into three, large, posteriorly directed trunks.

[*Vertebrae and ribs.*] There are 70 to 74 vertebrae of which 39 to 46 are abdominal and 26-32 caudal (HARDENBERG, 1930). The amphicoelous centra are perforated by the notochord. The anterior 2-3 centra are half the length of the centra behind them. Centra just behind the head show an irregular arrangement of interlacing grooves and ridges. Increasingly the midlateral longitudinal ridge is emphasized so that by the eighth to tenth centrum it forms a stout ridge that extends from anterior to posterior end of each centrum between deep dorsal and ventral depressions. The ventral surface of anterior centra exhibits a pair of slender, longitudinal grooves. Only a single groove is present on posterior abdominal and caudal centra. In dorsal view a thin, longitudinal ridge is developed on either side of a medial depression. (See GOSLINE, 1960, for figure and description of the caudal skeleton.)

Neural arch, epineural and epipleural ribs of the first and second vertebrae arise together from pits on the dorsal surface of these centra. Neural arches and epineurals of vertebrae posterior to the second arise from thin dorsal ridges of each centrum. Neural arches are fused to the centra and neural spines are fused to these arches. From the third to fifth centrum epipleurals are attached to neural arches. Epipleural ribs posterior to the fifth centrum are attached to small pits along the anterior border of the lateral ridge. Pleural ribs commence on the fourth centrum. These ribs are inserted near the lower, anterior end of each centrum. No parapophyses are present. The last 15 pleural ribs are attached to hemal arches rather than to the centra. Hemal arches fuse below attachment of pleural ribs and form a spatulate spine. WOODWARD (1903) showed pairs of hair-like processes dangling from the abdomen of *Chirocentrus*. These processes are ventral ends of pleural ribs which extend outside of the epidermis in a dried specimen. Interneurals are not present.

[*Pectoral and pelvic girdles.*] The extrascapular is triradiate. The ventral arm of this bone lies against the posterolateral flattened surface of pterotic. The anterodorsal arm projects over the lateral neurocranial ridge. The posterior arm lies lateral to the ventrolateral limb of the post-temporal. The post-temporal is also triradiate (Fig. 27). The ventrolateral limb meets the extrascapular. A narrow, elongate rod extends ventromedially from the medial post-temporal surface to meet the posterior protuberance on the intercalar. The third limb rises anteriorly over the epiotic. The flat, elongate, supracleithrum joins the medial wall of the post-temporal dorsally and lies lateral to the cleithrum ventrally.

The vertical and horizontal arms of the cleithrum are approximately equal in length. The anterior end of the horizontal arm curves ventrally over anterior end of coracoid. The paired cleithra are firmly joined to each other

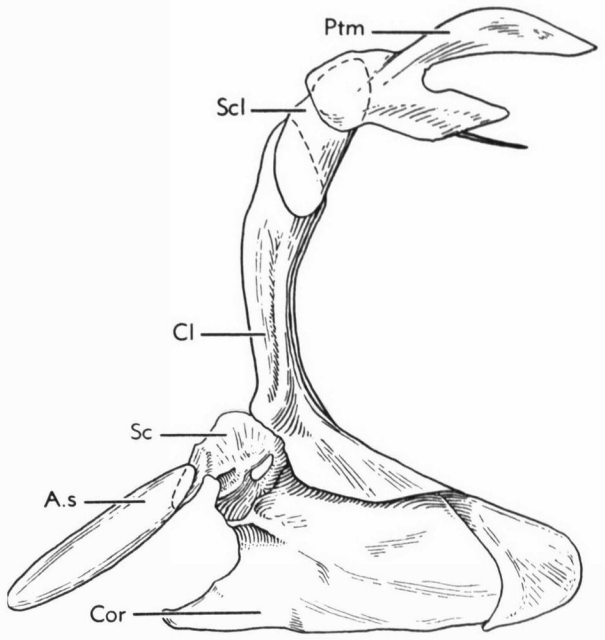

FIGURE 27. *Chirocentrus dorab* (FORSKÅL). Lateral view of pectoral girdle, ×1.25. [For explanation of abbreviations see p. 4.]

anterior to the coracoid. A wing of the horizontal arm extends ventrolateral to the coracoid.

The coracoid is a thin, dorsoventrally expanded plate which is united to the cleithrum dorsally. A slender process projects posteriorly from the ventroposterior end of this bone. Coracoids are firmly united forming a sharp keel ventrally. Midway along the posteroventral border of the coracoid a stout, a laterally directed articular facet is developed. The scapula is attached to this facet and to a wing of the coracoid dorsoanteriorly of this head. Ventroanterior to this facet a foramen pierces the coracoid. This foramen opens in a vertical plane.

The scapula joins the coracoid ventrally. Dorsally the scapula is united to the medial surface of the cleithrum at the junction between horizontal and vertical arms of the cleithrum. Two condyles are developed on the posterolateral margin of the scapula. The transversely concave upper condyle articulates with the first pectoral fin ray. The lower condyle, directly ventral to the upper one, is also transversely concave. This condyle is formed in part by the coracoid. The proximal pectoral actinosts articulate with this condyle. A prong of the scapula extends posteroventrally from the region of scapula-cleithrum junction. This prong supports a long, thin plate-like bone which lies above the pectoral fin. This bone was termed accessory scale by STARKS (1930) and postcleithrum by BERG (1940). I do not believe that it can be a postcleithrum because it has no connection with the cleithrum.

The mesocoracoid is a thin vertical strut attached dorsally to a thickened part of the cleithrum. Mesocora-

coid and coracoid join ventrally but the mesocoracoid does not meet the scapula.

The four proximal actinosts, firmly united by connective tissue, are not flattened longitudinally as STARKS (1930) stated. The first two present cup-shaped bases and articulate with the condyle formed by scapula and coracoid. The posterior two meet the scapula and coracoid ventromedial to this condyle. The first actinost is a single, stout ossicle. The second actinost comprises two ossicles. The proximal segments are T-shaped. The distal ossicle of the second actinost is a long, broadly rounded bone. The third and fourth actinosts also comprise two ossicles. The proximal ossicles of these two actinosts are elongate rods, the distal ossicles become broad distally. The distal ossicle of the fourth actinost caps the distal ossicle of the third actinost.

The pelvic girdle is less than 1 cm. long in a specimen of 35 cm. standard length. The basipterygia arch anterodorsally. Posterolaterally each basiptergium has a rounded facet for articulation of the pelvic fin. Three minute, flat, disc-shaped actinosts are present.

[*Fins.*] Dorsal and anal fin ray counts appear in the species diagnosis. The dorsal fin originates far back on the body posterior to the anal fin origin. The proximal segment of the proximal dorsal pterygiophore projects anteriorly.

The caudal fin consists of 10 principal dorsal and 9 principal ventral rays. All rays are segmented stepwise at an acute angle to the longitudinal axis.

The pectoral fin ray count is given in the species diagnosis. The broad, first ray exhibits a concave facet which articulates with the dorsal scapular condyle. The first pectoral ray constitutes a spine although distally incomplete transverse segmentation characterizes this ray. In cross section, dorsal and ventral sections of the first ray are still distinct but firmly united. All rays, except the first are divided longitudinally. This division begins more proximally on the posterior pectoral fin rays. These rays are all distally segmented.

The pelvic fin is slightly more than 1 cm. in length. Pelvic rays are segmented distally and, except for the first, divided longitudinally. Pelvic fin ray counts are given in the species diagnosis.

[*Scales.*] The scales of *Chirocentrus* are thin and extremely deciduous (Fig. 13,*G*). Mid-body scales are dorsoventrally elongate, approximately 2-4 mm. in height and 1-2 cm. in length in specimens of 35-40 cm. standard length. The only structures on these scales are fine microscopic circuli.

[*Soft anatomy.*] JACOBSHAGEN (1937) demonstrated that the so-called spiral valve comprises only the superficial and not muscular part of the mucosa.

[*Discussion.*] Separation of this species from *Chirocentrus nudus* is largely dependent on statistical differences (HARDENBERG, 1930). Range data in the diagnosis are based on 34 specimens.

CHIROCENTRUS NUDUS Swainson, 1838

See FOWLER (1941) for extensive synonymy prior to 1941.
Chirocentrus nudus SMITH, 1950, p. 87.
Holotype. Location not determined.
Geologic occurrence and distribution. Recent: India, Singapore, Indonesia (FOWLER, 1941).

Diagnosis. Based on HARDENBERG (1930) and FOWLER (1941). Elongate fishes. Maximum depth of trunk contained 5-5.25 times (range 5-7) in standard length. Head about 5.3 times (range 4.7-6.3 in standard length. Maximum depth of head included approximately 1.3 times in length of head. Snout contained 3.25-3.7 in head. Diameter of orbit contained 4.3-4.5 in head and 1.2-1.5 in snout. Posterior end of maxillary reaches beyond preoperculum. Gill rakers 4-5+16-17. Vertebrae about 70-72; 42-43 (range 39-45) abdominal and 28 (range 26-30) caudal. Rays of dorsal fin IV, 12-13; anal fin I-III, 28-32; pectoral fin I, 11-13; pelvic fin I, 5-6.

Discussion. Range data from HARDENBERG are based on 100 specimens.

?Family CHIROCENTRIDAE Saint-Seine, 1949

Genus PLATINX Agassiz, 1835

Platinx AGASSIZ, 1835, p. 304.
Type-species. Platinx macropterus (DE BLAINVILLE), 1818, p. 342.
Geologic occurrence and distribution. Lutetian (middle Eocene) Monte Bolca, Italy.

Diagnosis. Elongate fish attaining 0.5 m. in standard length. Head contained approximately 4.5 times; maximum body depth about 5.5 times in standard length. Head length exceeds maximum depth of trunk. Gape small, mouth cleft terminal, no trace of dentition. Vertebrae 69? Dorsal fin of approximately 20 rays begins just behind origin of anal fin which has about 20 rays. Pectoral fin longer than head. First pectoral fin ray spinous. Pelvic fin small, inserted at start of last sixth of distance between pectoral fin base and origin of anal fin.

Discussion. AGASSIZ (1835) first considered this fish a scombroid, later (1844) a halecoid. WOODWARD (1901) placed *Platinx* among the chirocentrids but included in this genus two other genera which are significantly different from *Platinx macropterus*. These genera, *Monopteros* and *Thrissopterus* are not chirocentrids (see section on "Species Formerly Considered Chirocentrids"). EASTMAN (1905), without presenting reasons, placed *Platinx* in the Albulidae, a position followed by ERASMO (1922). Recent authors (SCHAEFFER, 1947) and SAINT-SEINE (1949) who compared *Platinx* with other chirocentrids followed the diagnosis of WOODWARD (1901). This diagnosis includes structures pertaining to three distinct genera. For example, the dentition to which WOODWARD referred is based on *Monopteros*.

Body shape, position of unpaired fins, and size of pectoral fin suggest that *Platinx* may be a chirocentrid, but the mouth is small (EASTMAN, 1905) thus differing from chirocentrids. Examination of the cranium may require assignment of *Platinx* to another family.

PLATINX MACROPTERUS (de Blainville), 1818

Esox macropterus BLAINVILLE, 1818, p. 342.
Platinx elongatus AGASSIZ, 1835, p. 304; AGASSIZ, 1844, p. 125; BAS-

SANI, 1874, p. 188; WOODWARD, 1901, p. 89; LERICHE, 1906, p. 380.

Platinx macropterus EASTMAN, 1905, pl. 12; ERASMO, 1922, p. 70.

Platinx intermedius EASTMAN, 1905, p. 13, pl. 2, fig. 1; ERASMO, 1922, p. 70.

Holotype. Part and counterpart of complete fish. Lutetian, Monte Bolca, Verona, Italy. Paris, Musée National d'Histoire Naturelle, nos. 10964 and 10965.

Geologic occurrence and distribution. Same as the holotype.

Discussion. EASTMAN (1905) distinguished *Platinx intermedius* from *P. macropterus* by greater body depth relative to length, pectoral fin shorter than maximum depth of trunk and longer lobes of caudal fin. The holotype and only specimen of *P. intermedius* (Paris, Mus. Hist. Nat., 11014 and 11015) is much distorted. Bones of the head are displaced and the body scales have floated dorsally and ventrally giving a false impression of body depth. LEHMAN (personal communication) believes that *P. intermedius* is a dubious species. In view of the condition of the holotype, reasons cited by EASTMAN will not permit separation of *P. intermedius* from *P. macropterus.*

SPECIES FORMERLY CONSIDERED CHIROCENTRIDS

When originally described the genera and species cited in this section were referred to Chirocentridae or Ichthyodectidae, or were included in one of these families by a reviser. Present allocation of these species is indicated by reference to the latest revision. If no study of them has appeared subsequent to their original description, reasons for their removal from the Chirocentridae are given.

AGASSIZ (1844) assigned to *Thrissops* two species which WOODWARD (1895) transferred to the holostean family Pachycormidae. One, *Thrissops micropodius*, was placed in synonymy with *Euthynotus incognitus* (DE BLAINVILLE), the other generically reassigned as *Euthynotus intermedius* (AGASSIZ). WOODWARD also found that two other genera, *Heterothrissops* and *Pseudothrissops* named by SAUVAGE were synonymous with *Euthynotus.*

Thrissops molossus WOODWARD (1919) is based on a single specimen lacking dorsal part of the cranium, most of the body and fins, except the distorted lower half of the caudal. There is no cogent reason for including this fish in the chirocentrids. The position of the dorsal fin is unknown. The maxillary is elongate and shallow like that of elopids. The enlarged orbit is out of proportion to the head. This could be a young fish but its standard length of 27 cm. brings it within the size range of adult *Thrissops* of several species. The centra are not characterized by a longitudinal lateral ridge. Until better specimens clarify the anatomy of this species, it should remain incertae sedis.

WOODWARD (1901) suggested that *Eurystethus brogniarti* was related to *Thrissops.* ROMER (1945) and ARAMBOURG and BERTIN (1958) include *Eurystethus* among leptolepids.

Scales designated *Cladocyclus strehlensis* from the Upper Cretaceous of Strehlin, Poland, and near Prague, Czechoslovakia (GEINITZ, 1868, 1875; FRITSCH, 1878), are so varied in shape, position of radii and number of circuli as to leave no doubt that several genera and families are represented by these scales. Because FRITSCH described jaw elements from the same area belonging to *Xiphactinus* some of these scales might pertain to this genus but none of the figured scales resemble those of North American *Xiphactinus audax.* Teeth and scales referred to *Cladocyclus* sp. by TOULA (1905) are from lower Tertiary deposits near Vienna. Proper taxonomic affinity of these parts is undeterminable from the information given by TOULA.

None of the Upper Cretaceous scales from Turkestan described by ROMANOVSKY (1884, 1890) as *Cladocyclus strehlensis* and referred by COCKERELL (1919) to species of *Hypsodon* and *Ichthyodectes* pertain to chirocentrids. These round scales differ from chirocentrid scales in showing numerous circuli, no punctae and exhibiting anterior and posterior radii reaching the scale nucleus.

COCKERELL (1919) named two scales from the Upper Cretaceous Mesa Verde Formation of Wyoming *Hypsodon? radiatulus.* These are too strongly curved and antero-posteriorly flattened to represent this genus.

Portheus dunedinensis CHAPMAN (1934) comes from Abbotsford, near Dunedin, New Zealand. The single specimen, a crushed cranium differs from *Portheus* (in this study *Xiphactinus*) in several particulars. The quadrate-mandibular articulation lies behind the orbit rather than below the middle of the orbit. The blunt, short (5-9 mm.) conical teeth are plicate at the base in contrast to the smooth, larger teeth of *Xiphactinus.* The width of the mandible in ventral view is proportionally greater than in *Xiphactinus.* BENSON (1956, p. 16) cites a personal communication of E. I. WHITE in which the latter states that *P. dunedinensis* is "closely related to *Scombrinus* which characterizes Ypresian beds of the Thames estuary."

CASIER (1961) referred several teeth and vertebrae from the Mongala River in the Congo to the Chirocentridae. According to CASIER these fish remains are from the Lower Cretaceous above the Neocomian. These teeth are characterized by longitudinal folds not seen in chirocentrids. Vertebrae, approximately 3 cm. in transverse diameter, do not show the lateral ridge and grooves characteristic of Cretaceous chirocentrids.

Three genera from the Eocene of Monte Bolca, Verona, Italy, have been assigned at one time or another to different teleostean families including the Chirocentridae. One, *Monopteros gigas* VOLTA (1796), later changed to *Platinx gigas* (AGASSIZ, 1835), is represented by three specimens. VOLTA believed that this fish was a scombrid while AGASSIZ placed this genus with the halecoids. WOODWARD (1901) assigned *Platinx gigas* to the Chirocentridae whereas EASTMAN (1904, 1905) considered *Monopteros* the valid name and referred this genus to the Albulidae. *Monopteros gigas* attains a standard length of approximately 50 cm. The oval shaped body, unlike chirocentrids and albulids, resembles that of some sparoids. The head

contained approximately four times in standard length has a small mouth. Conical teeth line jaw margins and a series of molariform crushing teeth occur in the pharyngeal region (EASTMAN, 1904). Vertebrae number approximately 60 of which about half are caudal. Elongate pectoral fins exceed maximum body depth. Dorsal and anal fins are opposite each other. The caudal fin with long dorsal and ventral lobes is deeply forked.

Only the elongate pectoral fin and posterior position of the dorsal fin suggest that *Monopteros gigas* is a chirocentrid. EASTMAN justified inclusion in the Albulidae on the presence of molariform teeth, structure of caudal and "other fins." Considering body shape, position of the dorsal fin (which is near the middle of the body in albulids) and the elongate pectoral fin, *Monopteros gigas* differs from the Albulidae. Further study of these specimens is necessary to determine their true relationship.

The second genus from the Eocene of Monte Bolca is *Thrissopterus catullii* HECKEL (1856). The single specimen of this species is a narrow bodied, anguilliform fish slightly more than 20 cm. in standard length. The head is included 6 times and maximum body depth 10 times in standard length. The mouth is short; the quadrate-mandibular articulation lies below the anterior end of the orbit. There are approximately 71 centra. Abdominal centra show a longitudinal, lateral ridge between two deeply incised grooves. A thin ridge extends dorsally and ventrally from the center of this longitudinal ridge. The dorsal fin of 34 rays begins above first third of anal fin which has 38 rays. WOODWARD (1901) included *Thrissopterus* in *Platinx,* in having (1) an elongate slender body, (2) a ERASMO (1922), without giving reasons, placed *Thrissopterus* in the Albulidae. *Thrissopterus* differs from *Platinx* in having (1) an elongate slender body, (2) a longer head profile, (3) higher dorsal and anal fin ray counts, and (4) an elongate, five-rayed pectoral fin without a broad first ray. Profile of the head and small circumorbitals with a straight ventral margin suggest *Albula.* Gape of the mouth is short as in albulids. There is no indication of a palatine malleolus as in chirocentrids. Vertical ridges of abdominal centra differentiate *Thrissopterus* from chirocentrids and albulids. Reexamination of this specimen is necessary to determine proper familial affinity.

The third genus, *Coelogaster analis*, also from Monte Bolca, was described by EASTMAN (1905). AGASSIZ (1835), who first used this name, never published a description. WOODWARD (1901) suggested, without giving reasons, that this genus might be referred to the Chirocentridae, but EASTMAN placed it in the Abulidae. *Coelogaster* was used for a hymenopteran in 1780 (NEAVE, 1939) and hence is unavailable for this fish. Only a single specimen, elongate and scombriform in outline, is known. The head, included about 4 times in standard length, has a gently rounded outline. Most of the bones are displaced and fragmentary. Vertebrae number between 40-45. According to EASTMAN, the dorsal fin consists of two parts, an anterior of 9 rays and a posterior of 10 or more rays. Pelvic fins are small with 8 rays. The caudal fin is broad and lunate. These characteristics are not found among chirocentrids or albulids. Again, reexamination of the specimen is necessary in order to determine true relationships.

Chirocentrus polyodon GÜNTHER (1876) based on an incomplete upper and lower jaw from the Tertiary of Padang, Sumatra, has been referred to the Osteoglossidae and placed in synonymy with *Musperia radiata* (SANDERS, 1934).

BREDER (1942) suggested that *Chirocentrodon bleekerianus* GÜNTHER, an existing species from the Caribbean, is more closely related to the Chirocentrinae than Clupeinae with which it is usually placed. He supported chirocentrine association because of similarity in "skull and dental characters and general conformation." BREDER noted that *Chirocentrodon* like *Chirocentrus* has a palatine malleolus and an otic region of the neurocranium which resembles that of *Chirocentrus* as compared with *Clupea.* But *Chirocentrodon* differs from *Chirocentrus* in the presence of abdominal scutes and larger scales. BREDER was willing to overlook these differences in moving *Chirocentrodon* to the Chirocentridae. Study of an X-ray of *Chirocentrodon bleekerianus* kindly supplied by Dr. BREDER, shows that the dentary has a high coronoid crest as in *Clupea* and unlike *Chirocentrus.* There is no evidence of a stout parethmoid malleolus such as is found in chirocentrids. The presence of a living chirocentrid outside of the Indo-Pacific region would be zoogeographically significant in view of the wide distribution of chirocentrid fishes during the Cretaceous. But I believe that abdominal scutes remain an important character for separating clupeids and chirocentrids and, therefore, *Chirocentrodon* should be retained among the clupeids.

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